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BY

JOHN EDWARDS HILL

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BATS REFERRED TO *HESPEROPTENUS* PETERS, 1869 (CHIROPTERA: VESPERTILIONIDAE) WITH THE DESCRIPTION OF A NEW SUBGENUS

By J. E. HILL

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SYNOPSIS

Species currently allocated to the vespertilionid genus *Hesperoptenus* are reviewed in detail and divided into two subgenera, one, *Hesperoptenus* (*Milithronycteris*) with type species *Nycticejus tickelli* Blyth, 1851, proposed as new, to include also *H. blanfordi* (Dobson, 1877) and *H. tomesi* Thomas, 1905. The nominate subgenus contains only its type species *H. doriae* (Peters, 1869), here reported for the first time from Malaya, this being the second record of the species, hitherto known only from its holotype from Sarawak, Borneo.

INTRODUCTION

BATS of the Asiatic genus *Hesperoptenus* are, in general, rarely collected and therefore do not feature extensively in museum collections. Consequently, they remain for the most part rather poorly known and, apart from one Indian species, have received only scant attention in the literature. As it is currently recognized, *Hesperoptenus* is held to include four species, *doriae*, *tickelli*, *tomesi* and *blanfordi*. Their association together has been considered open to doubt by some authors while the most recent definition of the genus is based upon *tickelli* rather than upon the type species *doriae*. In this account the four species are examined and compared and although the number of specimens available remains small in some it has been possible nevertheless to describe the features of each species in detail and to discuss their differences and possible relationships. As a result, *Hesperoptenus* as previously understood is divided into two subgenera, one described as new.

HISTORY

The name *Hesperoptenus* was proposed by Peters (1869a : 626) for a subgenus of *Vesperus*, with type species *V.* (*H.*) *doriae* described concurrently from Sarawak, Borneo. Shortly afterwards, Peters (1869b : 638) described *V.* (*H.*) *kraussi* from Yoruba, Lagos, Nigeria, nowadays considered a synonym of *Glauconycteris poensis* (Dobson, 1878 : 255 ; Thomas, 1913 : 145 ; Rosevear, 1965 : 275). The two species described by Peters are figured together in his posthumous publication of illustrations of Chiroptera from the Zoologische Museum, Berlin (1906, pl. 26), and in this are referred to *Vesperus*, with no mention of *Hesperoptenus*.

Dobson (1876 : 112) in a monographic study of the Asiatic Chiroptera placed *doriae* in the genus *Vesperugo*, largely repeating the description by Peters, in translation. Dobson remarked that he thought *doriae* to be closely allied to *Vesperugo tickelli* (Blyth, 1851) and that when specimens of both could be compared it would be found that they could be included together in the subgenus *Hesperoptenus*. Later, Dobson (1877 : 312) described *Vesperugo* (*Hesperoptenus*) *blanfordi* and so implicitly recognized *Hesperoptenus* as a subgenus. Subsequently, he (1878 : 239) defined *Hesperoptenus* as a subgenus of *Vesperugo*, to include *doriae*, *tickelli* and *blanfordi*. In the same work (p. 255) Dobson reduced *Vesperus* (*Hesperoptenus*) *kraussi* Peters, 1869 to the synonymy of *Glauconycteris poensis*, where it has since remained. Eventually, *Hesperoptenus* as understood by Dobson was raised to generic rank (Jentink, 1887 : 278 ; 1888 : 182 ; Wroughton, 1897 : 723 ; Trouessart, 1897 : 116 ; 1904 : 83), with Thomas (1905 : 575) describing a fourth species, *tomesi*.

The essentials of the classification proposed by Dobson have persisted until the present day. Miller, the monographer of bat genera, retained (1907 : 211) generic rank for *Hesperoptenus* but examined only *tickelli*, which he employed as the basis for his generic diagnosis. This definition moved from the concept established by Dobson (1878 : 239), who, following Peters, had characterized the subgenus *Hesperoptenus* by 'outer upper incisors very small, scarcely raised above the gum, generally posterior to the toothrow ; penis with a distinct bone ; post-calcaneal lobe well-developed ; wings from the base of the toes'. Dobson had not seen *doriae* which he stated differed from *tickelli* and *blanfordi* in that the outer upper incisors were in the toothrow and not posterior to it as in these species. Miller (1907 : 211) diagnosed *Hesperoptenus* almost entirely by the features of the dentition, relying largely on the configuration and position of the upper incisors. Since, like Dobson, Miller did not examine *doriae*, he employed *Hesperoptenus* with some hesitation, considering that the description of *doriae* by Peters indicated certain features suggesting that it might be generically distinct from both *tickelli* and *blanfordi*. Miller did note, however, that peculiarities of the prepuce and the presence of a large bone in the penis might indicate (as Dobson had thought with regard to the os penis or baculum alone) that the three species formed a distinct group (Miller did not include *tomesi*, of which he appears to have been unaware) but remarked that the value of these characters was not then well understood.

More recently, Tate (1942 : 268) considered Miller correct in the supposition that more than one genus was involved, but was unable to study either *doriae* or *blanfordi*.

This author referred to the position of the outer upper incisor in *doriae* and suggested further that the specialized thumb of *blanfordi* might be an indication that it too differed widely from its supposed congeners. Ellerman & Morrison-Scott (1951 : 174), who drew attention to this situation, pointed out that the holotype of *doriae* apparently remained unexamined and that the genus *Hesperoptenus* might prove untenable in the sense in which it was then accepted. Davis (1962 : 42) referred a specimen from Sabah, Borneo, to *doriae*, noting that in this example the outer upper incisor was displaced posteriorly. This circumstance led Medway (1965 : 65) to consider that the type species thus conformed to the current generic definition, thereby rendering groundless the speculation by Ellerman & Morrison-Scott. The example from Sabah, however, does not represent the type species but instead should be referred to *tomesi*, of which it is a juvenile male (Hill, 1972 : 38 ; vide infra).

It is clear that the taxonomy of *Hesperoptenus*, so far unresolved, can be clarified only by the detailed examination of the holotype of *doriae*, upon which any interpretation of the genus must turn. The original description by Peters and a brief note of forearm length, colour and incisive dentition by Hill (1972 : 38) appear to be the only published accounts based upon direct examination of the holotype, which is in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa. This specimen, until recently the only definitively known example of the species, was examined also by Oldfield Thomas, who, in a copy of Dobson's *Catalogue of the Chiroptera in the Collection of the British Museum*, 1878, now in the Library of the British Museum (Natural History), has annotated the remark 'Specimen sent over 12/1901' to the account of *doriae*. Thomas has added manuscript notes on the external features, baculum and incisive dentition, with some measurements, to the account by Dobson. Shortly after the holotype was studied during the early preparation of this paper, a second specimen of *doriae* was obtained quite by chance in Malaya by Lord Medway, almost exactly one hundred years after Peters first acknowledged the species.

Genus *HESPEROPTENUS* Peters, 1869

Hesperoptenus Peters, 1869a : 626 (as a subgenus of *Vesperus*). Type species *Vesperus* (*Hesperoptenus*) *doriae* Peters, 1869, from Sarawak, Borneo.

DIAGNOSIS. Similar to *Eptesicus* but differing from this genus in relatively wider palate with wide anterior emargination ; in the presence of well-developed basioccipital pits ; in larger, caniniform inner upper incisor (i^2), its basal area equal almost to one half that of the upper canine (c^1) ; and by the structure of the outer upper incisor (i^3) which is low, its tip reaching barely to the cingulum of i^2 or of c^1, with basin-like cingulum and low central cusp. Dentally similar to *Glauconycteris* but differing from this genus and from the closely related *Chalinolobus* in having the posterior margin of the ear terminating on the head at a point not much anterior to the insertion of the anterior margin, not extending almost to the corner of the mouth, and in the absence of a fleshy lappet on the lower lip near this point. The majority of species of *Hesperoptenus* differ further from *Eptesicus*, *Glauconycteris* and *Chalinolobus* in the marked inward displacement of i^3 from the toothrow.

DESCRIPTION. Muzzle low and wide, sparsely furred anteriorly; narial openings semi-lunate or nearly circular, opening sub-laterally; usually a small wart-like protuberance above the anterior canthus of the eye, bearing a few long whiskers; lower lip with broad median pad; a small naked or nearly naked area immediately beneath the symphysis menti, preceding a low wart which bears a few long hairs. Ear subquadrangular; anterior margin with rounded or very slightly pointed posteriorly directed basal lobe; tip of ear rounded; posterior margin with prominently developed antitragal lobe effecting a quadrate junction with the side of the head behind and level with the angle of the mouth, from which it is separated by a low wart bearing a few longer hairs. Tragus slightly hatchet-shaped, its upper part prolonged anteriorly. Metacarpals of third, fourth and fifth digits nearly equal in length, the third usually very slightly the longest; a well-developed post-calcarial lobe, sometimes supported by a cartilaginous spur; penis with wide, saccular prepuce with large terminal opening.

Skull with wide braincase, the frontal region not especially inflated; rostrum short; palate short, wide, the lateral margins of the pre-palatal emargination not extending greatly beyond the inner margins of the inner upper incisors (i^{2-2}) and separated from the canines (c^{1-1}) by a relatively wide ledge of bone; evident basioccipital pits. Dental formula $i\,\frac{2}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{1}{2}$, $m\,\frac{3}{3} = 32$; inner upper incisor (i^2) massive, caniniform, unicuspid, with prominent cingulum, the tips of the inner incisors inwardly directed and slightly convergent; outer upper incisor (i^3) low, with basin-like cingulum from which arises a small pyramidal cusp, extending barely to the cingulum either of i^2 or of the upper canine (c^1) in height; i^3 sometimes displaced inwardly from the toothrow to the extent that it may lie behind or almost behind i^2; third upper molar (m^3) reduced but retaining mesostyle, metacone and three commissures; third lower molar (m_3) usually only slightly reduced, its posterior triangle a little smaller than its anterior triangle, but considerably so in one species.

DISTRIBUTION. The genus is distributed through India, Sri Lanka, Burma and the Andaman Islands to Thailand and Malaysia, including Borneo.

Subgenus *HESPEROPTENUS* Peters, 1869

DIAGNOSIS. Ear and tragus membranaceous; second phalange of third digit markedly longer than first phalange; braincase slightly inflated, rather globose; rostrum not especially widened; supraorbital region only very slightly inflated; lower maxillary margin of orbit narrow, forming a narrow, tapering ledge alongside the toothrow; maxillary toothrows nearly parallel; outer upper incisor (i^3) in toothrow or nearly so, not markedly intruded.

DISTRIBUTION AND SPECIES. The subgenus is known so far only from Malaysia and includes solely the species *Hesperoptenus doriae* (Peters, 1869), described originally from Sarawak, Borneo, and here reported for the first time from Malaya.

Hesperoptenus doriae (Peters, 1869)

Vesperus (*Hesperoptenus*) *doriae* Peters, 1869a : 626. Sarawak, Borneo.
Vesperugo (*Vesperus*) *doriae*, Dobson, 1876 : 104, 122.
Vesperugo (*Hesperoptenus*) *doriae*, Dobson, 1878 : 239.
Vesperugo doriae, Dobson, 1880 : 187 ; Hose, 1893 : 40.
Vesperugo donriae Hose, 1893 : 40. Lapsus.
Hesperoptenus doriae, Trouessart, 1897 : 116 ; 1904 : 83 ; Miller, 1907 : 211 ; Chasen, 1940 : 52 ; Tate, 1942 : 269 ; Ellerman & Morrison-Scott, 1951 : 174 ; Davis, 1962 : 42 (erratum, based on *tomesi*) ; Medway, 1965 : 65 (erratum, based on *tomesi*) ; Hill, 1972 : 38.

HOLOTYPE. Adult male CE 40094 in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy. In alcohol, skull removed.

DESCRIPTION. Muzzle with a shallow longitudinal groove immediately behind the widely separated narial openings which are nearly circular ; a few sparse hairs along the upper lip between the nostrils, the internarial region otherwise nearly naked and with only a sparse covering of short hairs above the nostrils and internarial pad ; prominent wart above anterior canthus of eye, bearing a few long whiskers ; lower lip with a broad median pad with no more than a trace of a median dividing groove at its posterior border only ; a small naked area beneath the symphysis menti, preceding a low wart which bears a few long hairs. Ears (Pl. 1) membranaceous, not thick or fleshy, rounded, more or less subquadrangular, the external surface of the conch quite densely clothed with hair for about one half the length of the ear, a few sparse hairs on the inner surface ; anterior margin of ear strongly convex, with rounded, posteriorly directed lobe at its base ; tip rounded ; posterior margin shallowly concave distally but otherwise strongly convex ; well-developed, fleshy antitragal lobe thickened along its outer margin, terminating quadrately behind and level with the corner of the mouth but separated from it by a low wart bearing a tuft of longer hairs. Tragus (Figs 1a, 1b ; Pl. 1) membranaceous, about one half the length of the ear, its anterior margin straight proximally, concave distally ; tip rounded, directed anteriorly ; upper margin nearly horizontal, sloping only slightly posteriorly, curving convexly to the slightly convex posterior margin which has a large, more or less triangular lobe at its base.

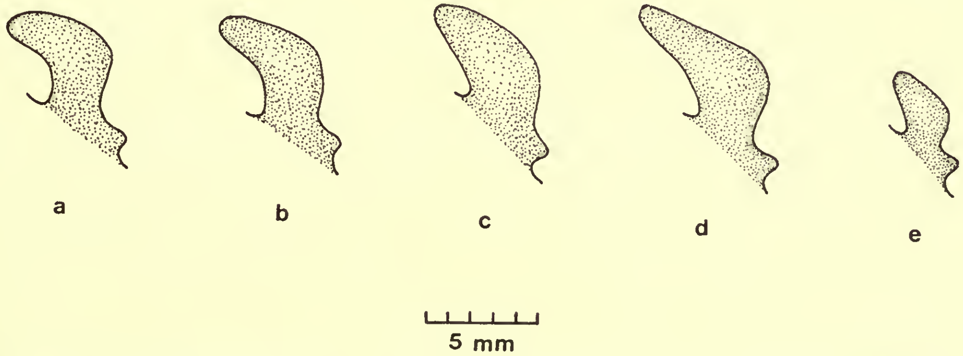

FIG. 1. Tragus of : (a) *Hesperoptenus doriae*, holotype, Sarawak ; (b) *H. doriae*, Malaya ; (c) *H. tickelli* ; (d) *H. tomesi*; (e) *H. blanfordi*.

Thumb long, its upper surface sparsely haired, with a strong claw ; forearm naked except for a few hairs proximally ; upper surface of tibia and of toes with a few scattered hairs ; fur extending sparsely on to the dorsal surface of the uropatagium for about one half its width, the ventral surface similarly but more thinly haired. Third metacarpal the longest, second and fourth very slightly shorter, the fifth the shortest ; second phalange of third digit longer than first phalange ; endopatagium and uropatagium slightly reticulated, remainder of flight membrane striated ; a rounded post-calcarial lobe supported by a poorly defined cartilaginous prop ; penis with saccular prepuce, sparsely haired, with V-shaped preputial opening. Holotype dorsally pale brown, hairs dark brown at the base but pale straw for much of their length, the ventral surface similar but paler, the specimen evidently much bleached by long immersion in alcohol. A second specimen (in alcohol) from Malaya is dark brown above and below, the membranes blackish brown.

Skull (Pl. 1) small, with inflated, slightly globose braincase, more elevated posteriorly than anteriorly, the frontal region slightly inflated ; slight lambdoid crests ; postorbital region sharply constricted ; rostrum short, narrow, with very slight supraorbital ridges, the supraorbital region only very slightly inflated ; a shallow depressed area immediately above anteorbital foramen ; anterior margin of orbit in frontal aspect sloping slightly inwards towards upper surface of rostrum ; shallow median rostral depression. Narial emargination wide, deep, extending posteriorly to a line joining the anterior edges of the anteorbital foramina, in the holotype V-shaped, with rounded apex, in a Malayan specimen U-shaped.

Zygomata slender ; anteorbital foramen closed by a narrow bar of bone ; lower maxillary margin of orbit narrow, not especially flange-like ; pre-palatal emargination wide, extending laterally a little beyond the inner faces of the inner upper incisors (i^{2-2}) and posteriorly to a line joining the posterior faces of the canines (c^{1-1}), rounded posteriorly, its lateral margins forming a narrow bony shelf. Palate rather short and wide, the maxillary toothrows nearly parallel ; post-palatal extension long, its lateral margins initially more or less parallel, with a slight convex expansion a little more than halfway along the extension, the margins then convergent, the hamulars convergent posteriorly ; post-palatal spine prominent, broad at the base. Soft palate (Fig. 2a) with five post-canine ridges, the first unbroken, the remainder each medianly divided, curved convexly on each side of the palate towards its centre. Basioccipital narrow, with deep, narrow basioccipital pits, separated by a narrow ridge, the bullae relatively large.

Baculum (Fig. 3a) of holotype damaged, but has evidently a long, relatively wide, flattened shaft with little sign of any pronounced upward curvature. At the base the baculum is expanded to form paired basal flanges, thick and massive, separated above and below by shallow median fissures. The shaft itself is parallel-sided ; in section its upper surface is slightly convex, the ventral surface in the proximal and central parts of the shaft slightly concave. Towards the tip the shaft is thickened vertically, the tip itself rounded

Inner upper incisor (i^2) caniniform, large, unicuspid, its basal area one half that of the upper canine (c^1), with prominent cingulum. Anterior face rounded, tooth with slight lateral edges, postero-lateral faces scooped out at each side of a posterior

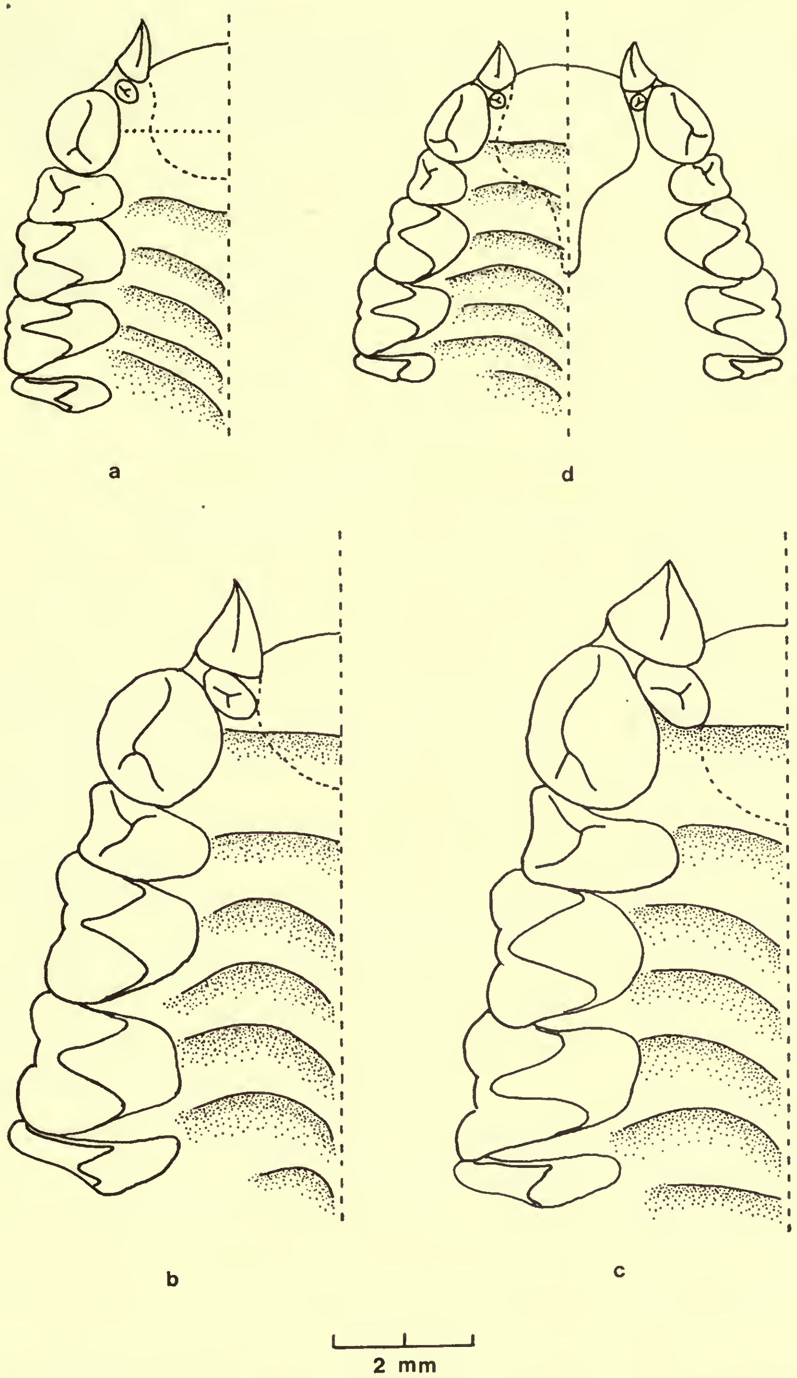

FIG. 2. Palate ridges of: (a) *Hesperoptenus doriae,* Malaya; (b) *H. tickelli*; (c) *H. tomesi*; (d) *H. blanfordi.*

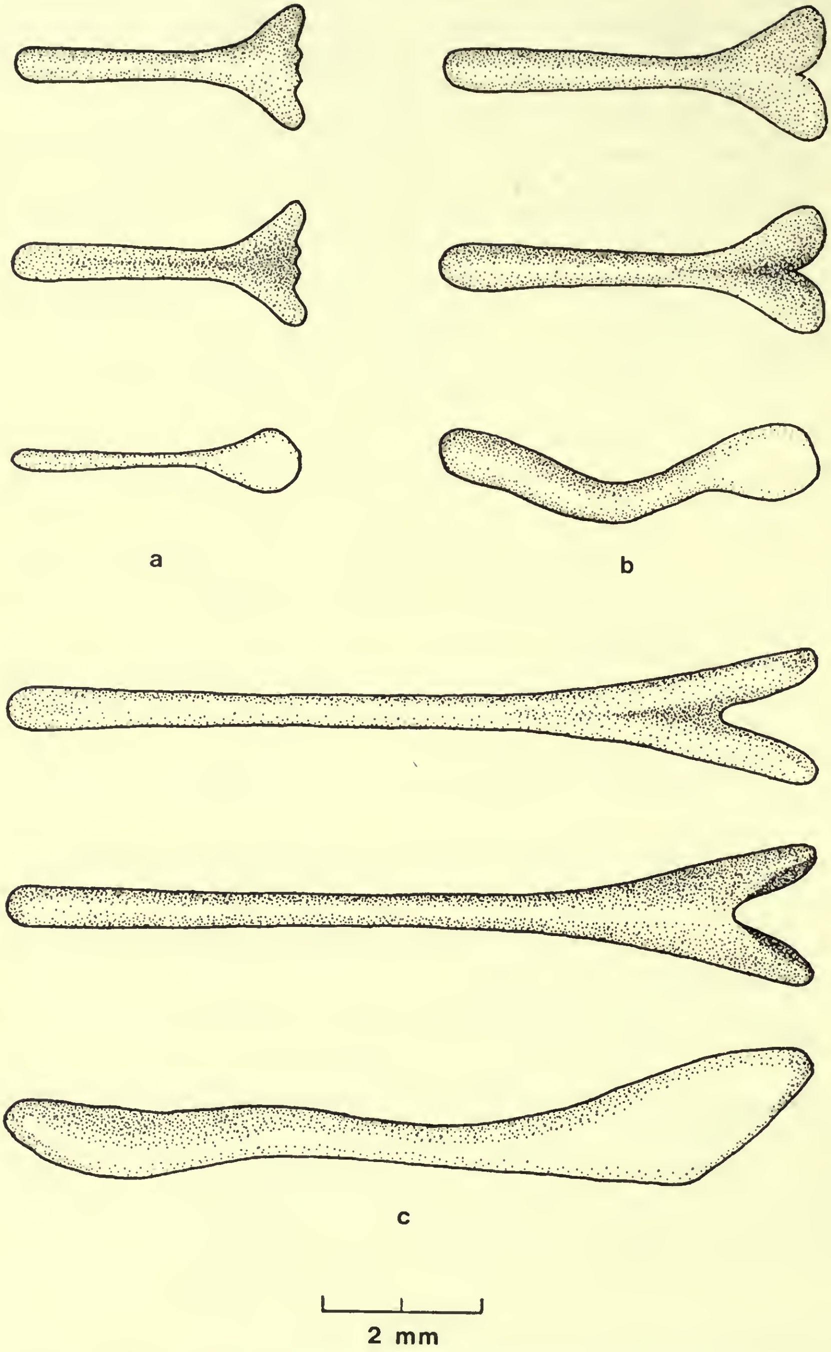

FIG. 3. Baculum of: (a) *Hesperoptenus doriae*, holotype; (b) *H. tickelli*; (c) *H. tomesi*, holotype.

median knife-like ridge. Outer upper incisor (i^3) simple, basal area little more than one quarter that of i^2, with basin-like cingulum and simple central cusp, i^3 basally slightly ovate, the longer axis lying diagonally to the toothrow; not displaced or only very slightly intruded, in contact or nearly so with i^2 and c^1, which is massive, with small anterior and posterior cingulum cusps. Upper premolar (pm^4) twice as wide as long, not compressed in the toothrow: first and second upper molars (m^{1-2}) with low hypocones, their lingual margins rounded; third upper molar (m^3) about one half crown area of m^1, with metacone and three commissures, the third not greatly reduced. Lower incisors (i_{1-3}) tricuspid, linear, slightly imbricated, i_3 a little thickened; anterior lower premolar (pm_2) about one third the crown area of the second lower premolar (pm_4); entoconid and hypoconid of third lower molar (m_3) not greatly reduced, one half the height of the anterior cusps, the tooth only slightly narrowed posteriorly (Pls 2 and 4d).

Measurements of the holotype and of a female example from Malaya appear in Tables 1 and 2.

DISTRIBUTION. MALAYA (Selangor); BORNEO (Sarawak). *Hesperoptenus doriae* is known apparently only from the holotype from Sarawak and from a female example (in alcohol, skull extracted) obtained by Lord Medway on 14 February 1969 at the Field Studies Centre, Ulu Gombok, Selangor, Malaya. This further specimen is now in the collections of the British Museum (Natural History). No direct comparison with the holotype has been possible but as far as can be determined the two specimens are in close agreement except for the more rounded, less angular narial emargination of the Malayan example.

REMARKS. The inflated, slightly globose braincase of *H. doriae* removes it rather sharply from *Eptesicus* and suggests *Glauconycteris* or the closely allied *Chalinolobus*, which are thought to be subgenerically related by Ryan (1966 : 86, 89) and by Koopman (1971 : 1). However, these differ from *Hesperoptenus* in the insertion of the posterior margin of the ear and in the presence of a lappet on the lower lip near the angle of the mouth, and the rostrum in general is more shortened. Externally, *H. doriae* is strongly reminiscent of *Eptesicus* or *Pipistrellus* and indeed its baculum is of the long-shafted type associated with the latter genus. Dentally, the species has some features in common with *Glauconycteris* in which the outer upper incisor (i^3) has a wide cingulum with simple central cusp and stands in the toothrow, although in some species a small degree of extrusion is found, to approach the condition usual in *Chalinolobus* in which the four upper incisors lie on a line in most species. In *H. doriae* the tendency is for i^3, although in the toothrow, to lie towards its inner or lingual border: the inner margins of the inner upper incisor (i^2), of i^3 and of the upper canine (c^1) lie on a line, with the outer margins of i^2 and c^1 extending considerably beyond the outer margin of i^3. Although on occasion a similar situation occurs in *Glauconycteris* (cf. *G. gleni*, vide Peterson & Smith, 1973 : 3, fig. 2, centre) the tendency in this genus seems to be for i^3 to become extruded. *Hesperoptenus doriae* differs further from *Glauconycteris* in its rounded and not linear postcalcarial lobe and in having the second and third lower incisors (i_{2-3}) linear and imbricated, lacking any low posterior cusp, rather than standing along the line of the

TABLE 1

External measurements (in mm) of *Hesperoptenus*

	H. doriae		*H. tickelli*			*H. tomesi*			*H. blanfordi*		
	Holotype ♂, Genoa Museum CE 40094 Sarawak	♀, BM 75.1873 Malaya	n	Range	Mean	Holotype ♂, BM 7.1.1.428 Malaya	♂, BM 74.455 Malaya	♀, BM 74.456 Malaya	n	Range	Mean
Length of forearm	38·0	41·1	44	49·1–60·3	54·0	51·0†	50·3	51·2	6	25·2–28·4	26·6
Length of thumb (with claw)	8·1	8·3	6	12·1–13·2	12·9*	11·5†	11·8	12·0	3	4·0– 4·3	4·2
Length of II^{m}	35·9	39·4	6	47·3–54·1	49·4*	45·0†	46·4	45·9	3	24·0–24·4	24·2
Length of III^{m}	36·8	39·5	6	48·0–53·6	50·1*	47·3†	47·8	47·2	3	25·2–26·3	25·7
Length of III^{1}	15·6	17·8	6	21·1–25·0	22·4*	21·9†	22·5	23·0	3	13·1–15·0	13·8
Length of III^{2}	19·0	21·3	6	21·8–25·0	22·8*	15·8†	16·8	16·5	3	8·0– 9·1	8·6
Length of IV^{m}	36·0	38·3	6	47·6–51·8	49·5*	47·3†	47·7	46·8	3	24·3–26·3	25·4
Length of V^{m}	34·8	36·8	6	47·3–52·0	48·9*	44·0†	44·1	44·6	3	23·2–25·4	24·4

n, number of specimens.

* Specimens from Sri Lanka only: no Indian examples in alcohol available.

† From dry skin.

The nomenclature for the digits in this table and in Table 3 follows a convention where, for example, III^{m} is the metacarpal of the third digit, III^{1} and III^{2} its first and second phalanges.

Table 2

Cranial measurements (in mm) of *Hesperoptenus*

	H. doriae		*H. tickelli*			*H. tomesi*			*H. blanfordi*		
	Holotype ♂, Genoa Museum CE 40094 Sarawak	♀, BM 75.1873 Malaya	n	Range	Mean	Holotype ♂, BM 7.1.1.428 Malaya	♂, BM 74.455 Malaya	♀, BM 74.456 Malaya	n	Range	Mean
Greatest length of skull	14·2	14·4	25	17·2–19·9	18·9	–	21·4	21·1	4	12·7–13·2	13·0
Condylocanine length	13·2	13·7	29	17·4–19·7	18·5	–	20·3	19·8	5	11·8–12·5	12·1
Condylobasal length	13·3	13·6	28	17·0–19·6	18·2	–	20·2	19·6	5	11·7–12·4	12·0
Length orbit–gnathion	2·8	2·9	30	4·5– 5·2	4·9	5·0	5·4	5·1	5	2·9– 3·2	3·0
Width across anteorbital foramina	–	4·4	31	6·5– 7·9	7·2	7·7	8·1	8·0	6	4·8– 5·3	5·1
Width across front of orbits	5·7	5·8	29	8·9–10·3	9·5	9·9	11·1	10·4	6	5·8– 6·5	6·1
Width across supraorbital swellings	5·0	5·2	28	7·5– 8·8	8·0	9·4	10·1	9·7	5	5·9– 6·3	6·2
Zygomatic width	9·1	–	18	13·3–15·3	14·2	–	15·5	15·2	1	8·7	
Postorbital width	3·9	4·1	30	4·5– 5·4	4·9	6·0	5·8	6·0	6	4·3– 4·7	4·5
Width of braincase	7·5	7·9	26	9·4–10·7	9·9	–	10·7	10·7	6	7·0– 7·5	7·2
Height of braincase	5·6	5·8	27	6·4– 7·1	6·7	–	7·6	7·6	6	4·6– 5·0	4·9
Mastoid width	8·1	8·5	24	10·4–12·1	11·2	–	12·2	12·2	5	7·5– 8·0	7·7
$c^1–c^1$	4·9	5·1	29	6·1– 7·2	6·6	7·5	8·1	7·8	5	4·0– 4·4	4·2
$m^3–m^3$	5·9	6·2	30	8·5–10·2	9·3	9·9	10·2	10·1	5	5·9– 6·3	6·1
$c–m^3$	4·5	4·6	34	7·0– 8·1	7·5	8·2	8·3	7·7	5	4·2– 4·4	4·3
Length of complete mandible	9·0	9·5	24	13·4–15·7	14·5	15·5	15·6	15·2	2	8·5, 9·6	
Length of right ramus	–	10·2	28	13·9–16·1	14·9	16·2	16·3	16·0	5	8·8–10·1	9·2
$c–m_3$	4·9	5·0	31	7·9– 9·1	8·3	9·3	9·5	8·8	5	4·5– 4·9	4·7

n, number of specimens.

toothrow with a low supporting cusp behind the central one of the three incisive cusps either of i_2 or of i_3. It differs quite sharply from *Chalinolobus* in the presence of a triangular lobule at the base of the posterior margin of the tragus rather than a low convexity; in its broad, saccular rather than smooth, prepuce which has a rounded, slightly V-shaped, preputial orifice and not a narrow vertical aperture; in wide, not narrow, pre-palatal emargination; in the structure of i^3, a simple cusp with broad cingulum rather than a broader, hollowed tooth and in the position of this tooth in the row rather than extruded from it. Despite some similarities, therefore, there appears to be no direct connection between this species and consequently *Hesperoptenus* with either *Glauconycteris* or *Chalinolobus*.

Hesperoptenus doriae differs sufficiently from the other species hitherto assigned to the genus as to justify their separation in a distinct subgenus. For this I propose:

MILITHRONYCTERIS subgen. nov.

TYPE SPECIES. *Nycticejus tickelli* Blyth, 1851.

INCLUDED SPECIES. *Vesperugo* (*Hesperoptenus*) *blanfordi* Dobson, 1877; *Hesperoptenus tomesi* Thomas, 1905.

ETYMOLOGY. The name of this newly separated subgenus has been chosen to commemorate the late G. S. Miller, the monographer of bat genera, at one time of the United States National Museum, now the National Museum of Natural History, Washington. The name is derived from *μυλωθρσς*, a master miller, and *νυκτερις*, a bat.

DIAGNOSIS. Like *Hesperoptenus* (*Hesperoptenus*) but ears and tragus fleshy rather than membranaceous; second phalange of third digit reduced, its length about equal to or less than the length of the first phalange; braincase lacking any marked inflation, elongate rather than globose; rostrum much broadened supraorbitally; lower maxillary margin of orbit heavy, flange-like, viewed ventrally forming a wide ledge alongside the toothrow; maxillary toothrows convergent anteriorly; and outer upper incisor intruded from toothrow to the extent that on occasion it may lie behind the inner upper incisor.

DESCRIPTION. Similar externally to *Hesperoptenus* (*Hesperoptenus*) but internarial region sometimes densely covered with short hairs; facial warts sometimes low and imperceptible; ear and tragus fleshy, the tip of the tragus sometimes considerably attenuated and prolonged anteriorly.

Skull with uninflated, elongate, slightly broadened braincase; frontal region barely elevated, the cranial profile straight or nearly so; rostrum relatively short, wide, the supraorbital region inflated and swollen; rostral depression very shallow or absent; an almost imperceptible depressed area immediately above the anterior part of the orbit; anteorbital foramen large; lower maxillary margin of orbit wide, flange-like; narial emargination deep, rounded posteriorly; pre-palatal emargination deep, wide, its lateral margins extending beyond the inner faces of the inner upper incisors (i^{1-1}), extending posteriorly to or almost to a line joining the posterior faces of the upper canines (c^{1-1}) ; post-palatal extension short, wide, with prominent median spine ; shallow but evident basioccipital pits ; bullae of moderate size.

Dentition much as in the nominate subgenus but outer upper incisor (i^3) intruded from toothrow so that the centre of the tooth lies almost exactly behind the centre of the inner upper incisor (i^2), with its anterior face lying approximately on a line joining the anterior faces of the upper canines (c^{1-1}), the tooth in contact or nearly in contact with the posterior face of i^2 and with the antero-internal face of c^1 ; anterior lower premolar (pm_2) about one half or a little less the basal area of the second lower premolar (pm_4), slightly compressed in the toothrow.

Distribution. India, Sri Lanka and the Andaman Islands east to Thailand, Malaya and Sabah, Borneo ; possibly occurs also in China.

Remarks. As here understood, the subgenus *Milithronycteris* includes three species, *tickelli*, *tomesi* and *blanfordi*. The larger species *tickelli* and *tomesi* are clearly more closely related to each other than either is to the very much smaller *blanfordi*, from which they differ quite sharply in a number of features. Nevertheless, in *blanfordi* as in the larger species, the braincase is broad, low and elongate, the rostrum expanded supraorbitally, with a broad sub-orbital flange, and the outer upper incisor (i^3) is intruded to lie behind the inner tooth (i^2). The three species may be keyed :

1 Large, length of forearm 48·6–60·0 mm 2
– Small, length of forearm 25·9–27·5 mm . . . . **blanfordi** (p. 21)
2 Dorsally yellowish brown to straw brown, ventrally a little paler ; anterior dentition to premolars not especially massive ; lower incisors (i_{1-3}) not greatly imbricated **tickelli** (p. 15)
– Rich chocolate brown both dorsally and ventrally ; anterior dentition to premolars heavy and massive ; lower incisors (i_{1-3}) much imbricated . . . **tomesi** (p. 19)

Hesperoptenus tickelli (Blyth, 1851)

Nycticejus isabellinus Kelaart (ex Blyth), 1850 : 317 (pagination of reprint of 1890). Nomen nudum. Sri Lanka.

Nycticejus tickelli Blyth, 1851 : 157. 'Central India, Ceylon and the intervening hilly country.' Restricted to Chaibassa, Bihar (Anderson, 1881 : 132, Wroughton, 1918 : 593).

Nycticejus isabellinus Horsfield (ex Blyth), 1851 : 38. Central India.

Nycticejus tickelli, Kelaart, 1852 : 24 ; Wagner, 1855 : 765, footnote, 766 ; Blyth, 1863 : 31.

Nycticejus isabellinus, Kelaart, 1852 : 24 ; Wagner, 1855 : 765, footnote ; Fitzinger, 1870 : 363 ; Dobson, 1876 : 113 ; 1878 : 240 ; Blanford, 1891 : 317.

N. [*ycticejus*] *isabellinus*, Blyth, 1863 : 31.

Nycticejus tickellii Fitzinger, 1870 : 362. Lapsus.

Vesperugo (*Vesperus*) *tickelli*, Dobson, 1876 : 104, 113, figs a, b, 208.

Vesperugo (*Hesperoptenus*) *tickelli*, Dobson, 1877 : 312 ; 1878 : 239, 240, pl. 12, fig. 3.

Vesperugo (*Hesperopterus*) (sic) *tickelli*, Anderson, 1881 : 132.

Vesperugo tickelli, Sterndale, 1884 : 63 ; Blanford, 1891 : 317, fig. 97.

Hesperoptenus tickelli, Jentink, 1887 : 278 ; Wroughton, 1897 : 723 ; Trouessart, 1897 : 116 ; 1904 : 83 ; Thomas, 1905 : 575 ; Miller, 1907 : 211 ; Wroughton, 1912 : 1180 ; 1913 : 37 ; 1915a : 86 ; 1915b : 103 ; 1917 : 66 ; 1918 : 593 ; Phillips, 1932a : 345 ; 1932b : 349 ; 1932c : 133 ; 1932d : 137 ; 1933 : 240 ; 1935 : 118 ; Tate, 1942 : 269 ; Ellerman & Morrison-Scott, 1951 : 174 ; Brosset, 1962 : 729 ; Hill, 1967 : 7 ; Hill & Thonglongya, 1972 : 191.

Hesperoptenus tickelii Jentink, 1888 : 182. Lapsus.
[*Hesperoptenus*] *isabellinus*, Trouessart, 1897 : 116.
Hesperoptenus isabellinus, Tate, 1942 : 269.

SYNTYPES. Dobson (1876 : 114 ; 1878 : 241) stated 'Type in the collection of the Indian Museum, Calcutta' but did not designate a specimen. Anderson (1881 : 132) listed as types three specimens in the Indian Museum. These are skins from Cháibasá (= Chaibassa, Bihar, India) presented in 1842 by S. R. Tickell to the Asiatic Society of Bengal, whose Museum later became a part of the Indian Museum. Listed as 156a–c by Anderson (1881 : 132) in the Indian Museum collections, these specimens are numbered 95A–C in Blyth's Catalogue (1863 : 31) of the mammals in the Museum of the Asiatic Society of Bengal and by Dobson (1876 : 208) as 474–476 in a catalogue of the specimens of Chiroptera in the collection of the Indian Museum which he provided in his *Monograph of the Asiatic Chiroptera*. Blyth (1863 : 31) also listed without data a skull (95D) later recorded (as 477) by Dobson (1876 : 208) as having the same data as the three skins, but Anderson (1881 : 132) lists this skull (as 156d) without locality but as originating from S. R. Tickell in 1842.

OTHER TYPE MATERIAL. Horsfield (1851 : 38) lists only a single specimen under *Nycticejus isabellinus*, a dried example from Central India, in the Museum of the Honourable East India Company, presented by the Asiatic Society of Bengal. There is little doubt that this specimen is that now registered as BM 60.5.4.12, presented to the British Museum (Natural History) by the Secretary of State for India, and from the East India House collection. It is a skin with skull in situ, but with the upper incisors visible, labelled in Blyth's handwriting '*Nycticejus isabellinus* Bl. Central India' and by Dobson '*Vesperugo tickelli*, Blyth. Syn. *V. isabellinus*, Blyth'. The specimen is therefore apparently the holotype of *Nycticejus isabellinus* Horsfield, 1851 : it exactly resembles *Hesperoptenus tickelli* as Dobson recognized.

DESCRIPTION. Muzzle much as in *Hesperoptenus doriae*, the longitudinal depressions behind nostrils shallow and faint ; membrane of ear and tragus thick and fleshy, fur extending densely on outer surface of conch for about one half the length of the ear, the inner surface with a few sparse hairs ; anterior margin of ear with a well-developed, slightly pointed posteriorly directed basal lobe ; proximally the anterior margin is strongly convex, distally nearly straight, the tip of the ear broadly rounded, the posterior margin convex. Tragus (Fig. 1c) about one half the length of the ear, slightly hatchet-shaped, widest at about one half its length, its tip narrow, rounded, anteriorly directed, the upper margin nearly horizontal, then sharply convex to join the rather less convex posterior margin.

Thumb relatively long, with a slight sprinkling of short hairs along its dorsal surface and with a strong claw ; forearm naked ; dorsal surface of tibia and foot with a few sparse, short hairs ; fur extending very sparsely on to the dorsal surface of the uropatagium for about one half its width, its ventral surface with a few scattered short hairs ; metacarpals of approximately equal length but the third usually slightly the longest ; post-calcarial lobe linear or slightly rounded at its central point, lacking a cartilaginous support; penis saccular, with U-shaped preputial opening.

Dorsally yellowish brown to straw brown, brighter posteriorly than anteriorly, the ventral surface similar but paler. Specimens from Sri Lanka and the Andaman Islands are a little darker than are those from the Indian mainland, and are more reddish brown dorsally, especially posteriorly. They also average a little smaller than those from the mainland. The differences, however, are small and scarcely justify subspecific recognition: in any event, specimens from Thailand are similar to Indian examples in colour but in size to those from Sri Lanka and the Andaman Islands. The differences in size are compared in Table 3.

TABLE 3

Dimensions (in mm) of *Hesperoptenus tickelli* from India, Sri Lanka, the Andaman Islands and Thailand

	Length of forearm					Condylobasal length				
	n	Range	Mean	s.d.	s.e.	n	Range	Mean	s.d.	s.e.
India	15	54·3–60·0	57·13	1·92	0·51	11	18·3–19·6	18·96	0·38	0·12
Sri Lanka	25	49·1–56·8	52·24	1·80	0·36	13	17·0–18·3	17·70	0·42	0·12
Andaman Islands		51·1					18·5			
Thailand	3	52·8–54·2	53·43			3	17·8–18·0	17·90		

	m^3–m^3					c–m^3				
	n	Range	Mean	s.d.	s.e.	n	Range	Mean	s.d.	s.e.
India	12	8·9–10·2	9·60	0·38	0·11	12	7·3–8·1	7·79	0·26	0·08
Sri Lanka	13	8·5– 9·5	9·07	0·28	0·08	17	7·1–7·7	7·38	0·19	0·05
Andaman Islands		8·8, 8·9					7·2, 7·2			
Thailand	3	9·1– 9·3	9·23			3	7·3–7·6	7·40		

n, number of specimens; s.d., standard deviation; s.e., standard error of mean.

Skull (Pl. 3a–c) large, with well-developed sagittal and lambdoidal crests, the braincase broad, uninflated; postorbital region sharply constricted, its width less than the width across the canines at the alveoli; supraorbital region considerably expanded, the supraorbital ridges terminating in small inflations; anterior orbital margin sharply defined, in frontal view sloping slightly inwards; anteorbital foramen of moderate size, enclosed by a moderate bony bar; maxillary margin of orbit heavy, flange-like; zygomata slender; narial emargination usually V-shaped but with rounded apex, sometimes more or less U-shaped; post-palatal extension short, with widely based but otherwise narrow median spine. Soft palate (Fig. 2b) with six post-canine ridges, the first two unbroken, remainder curving convexly to the median line, the last small, not reaching laterally to the teeth. Basioccipital pits large, shallow, sharply incised into the basisphenoid.

Baculum (Fig. 3b) with strong upward deflection, its shaft long, nearly parallel-sided, curved upwards at its middle part, its tip unthickened, rounded, shaft slightly narrowed towards the base, the basal part of the baculum expanded to form paired basal flanges, separated above and below by median V-shaped fissures.

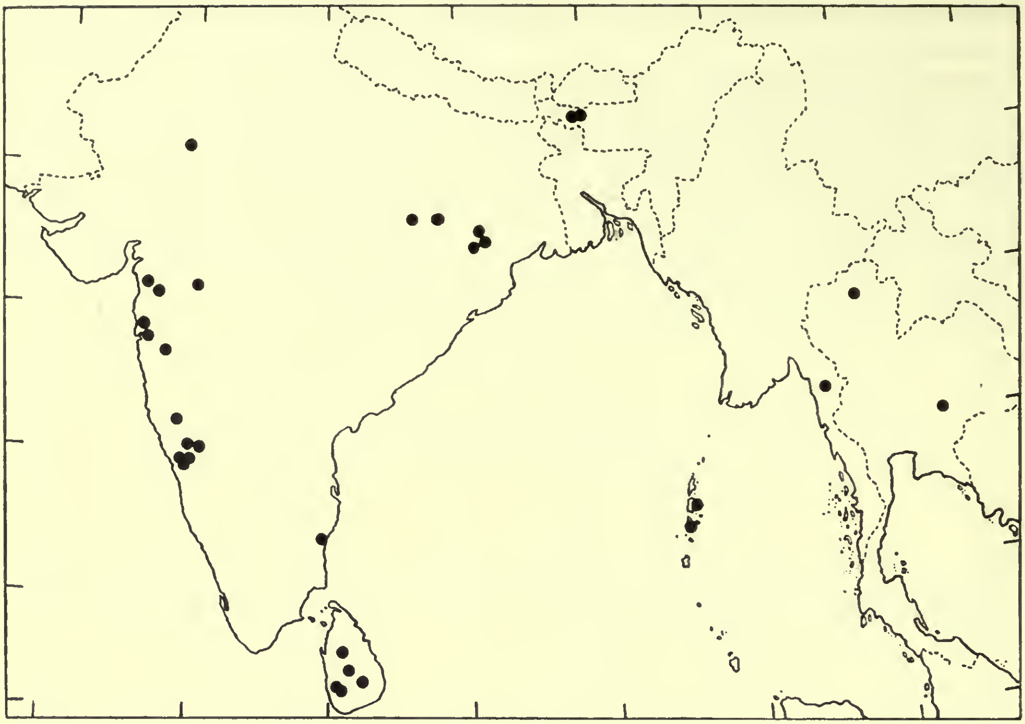

FIG. 4. *Hesperoptenus tickelli*, distribution.

Outer upper incisor (i^3) ovate, with wide, basin-like cingulum and three-faced cusp ; labial part of tooth interposed between inner upper incisor (i^2) and canine (c^1) but tooth otherwise intruded from row, its anterior face in contact with the posterior face of i^2 and lying on or a little in advance of a line joining the anterior faces of c^{1-1}, its postero-lateral face in contact or nearly so with the antero-lateral face of c^1 ; i^2 and c^1 separated by a narrow space equal to or a little less than one half the basal diameter of i^2, the centre of i^3 lying in advance of a line joining the centres of c^{1-1} ; lower incisors (i_{1-3}) thick but linear, not greatly imbricated, i_3 not especially massive (Pls 3a, c, 4e).

Measurements of *Hesperoptenus tickelli* appear in Tables 1 and 2.

DISTRIBUTION (Fig. 4). INDIA (Rajasthan : Dobson, 1878 : 241 ; Blanford, 1891 : 317. Uttar Pradesh : Wroughton, 1913 : 37. West Bengal : Wroughton, 1917 : 66. Bombay, Dobson, 1878 : 241 ; Wroughton, 1897 : 723 ; Brosset, 1962 : 729. Madhya Pradesh : Dobson, 1876 : 114, 208 ; Anderson, 1881 : 132, 133 ; Sterndale, 1884 : 63. Bihar : Dobson, 1876 : 114, 208 ; Anderson, 1881 : 132 ; Sterndale, 1884 : 63 ; Wroughton, 1915b : 103. Madras, Wroughton, 1918 : 593. Mysore : Wroughton, 1912 : 1180. Andaman Islands : Dobson, 1876 : 208 ; Anderson, 1881 : 132 ; Hill, 1967 : 7). SRI LANKA (Kelaart, 1850 : 317 (separate pagination) ; 1852 : 24 ; Blyth, 1863 : 31 ; Dobson, 1878 : 241 ; Wroughton, 1915a : 86 ; Phillips, 1932a : 345 ; 1932b : 349 ; 1932c : 133 ; 1932d : 137 ; 1933 : 240 ; 1935 :

118). BURMA (Dobson, 1877 : 312 ; Anderson, 1881 : 133 ; Blanford, 1891 : 317). THAILAND (Hill & Thonglongya, 1972 : 191). CHINA (Jentink, 1887 : 278 ; 1888 : 182, from 'Kolongsu', not traced).

REMARKS. *Nycticejus isabellinus* Horsfield, 1851. Initially a manuscript name from Blyth, *isabellinus* is validated by Horsfield (1851 : 38) (contrary to the assertion by Blanford, 1891 : 317, who says of this citation 'no description') with the remark 'Of the size of *N. temminckii* [= *Scotophilus kuhlii*], clearly characterised by an uniform isabellina tint both above and underneath'. The earliest use of *isabellinus*, by Kelaart (1850 : 317, pagination from a reprint dated 1890, in the British Museum (Natural History), differing apparently from the original), is without description in a Catalogue of mammals from Sri Lanka. Kelaart (1852 : 24) and Blyth (1863 : 31) list it as a synonym of *tickelli*, as does Fitzinger (1870 : 362), Dobson (1876 : 113 ; 1878 : 240), Blanford (1891 : 317) and Trouessart (1897 : 116). Tate (1942 : 269) listed it in parentheses as [*Hesperoptenus isabellinus* (Horsfield)] and repeated the description by Horsfield.

The names *Nycticejus tickelli* Blyth and *Nycticejus isabellinus* Horsfield both appeared in 1851. In neither of the publications concerned, the *Journal of the Asiatic Society of Bengal* or Horsfield's *Catalogue of the Mammalia in the Museum of the Hon. East-India Company* does there appear evidence to establish a definite date of publication. All that can be said is that the latter certainly appeared after 18 August 1851, the date of its prefatory list of contributors to the Museum ; Blyth's description is in the second issue of the four of the Journal for that year and probably appeared before the account by Horsfield. In these circumstances the name adopted is that employed by the first reviewer, namely Dobson (1876 : 113) ; Fitzinger (1870 : 362) gave a detailed description of the species and might be considered a prior reviewer.

Hesperoptenus tomesi Thomas, 1905

Hesperoptenus tomesi Thomas, 1905 : 575. Malacca, Malaya.
Hesperoptenus tomesi, Kloss, 1908 : 158 ; Chasen, 1940 : 53 ; Tate, 1942 : 269 ; Medway, 1969 : 38 ; Hill, 1972 : 38.
Hesperoptenus doriae, Davis, 1962 : 42 ; Medway, 1965 : 65.

HOLOTYPE. Adult male BM 7.1.1.428. Skin and skull, rear and lower part of cranium missing. From the Tomes Collection.

DIAGNOSIS. Muzzle a little more densely haired than in *H. tickelli* ; tragus (Fig. 1d) slightly more acutely pointed and directed a little further anteriorly ; differs sharply in rich, dark chocolate brown coloration both above and below ; skull larger with more prominent supraorbital ridges terminating in small tubercles ; anterior orbital margin more nearly vertical ; zygomata more widely expanded ; cingulum of outer upper incisor (i^3) a little narrower, tooth further intruded from row and only a little interposed between the inner upper incisor (i^2) and the canine (c^1).

DESCRIPTION. Apart from colour the external features of *H. tomesi* resemble those of *H. tickelli* very closely ; the metacarpals are a little more graduated, with the third the longest, the fourth usually a little shorter, and the fifth the shortest, although the differences in length are small. The post-calcarial lobe has a rounded central part but is otherwise linear, and lacks a cartilaginous supporting prop; the thumb, forearm and tibia are naked or nearly so.

Skull (Pl. 3d–f) similar to that of *H. tickelli* but braincase a little more elevated, especially posteriorly, with a more pronounced occipital 'helmet'; postorbital region narrow, its width less than the width across the upper canines (c^{1-1}) at the alveoli; anterior orbital margin heavy, flange-like, more sharply defined than in *tickelli*; anteorbital foramen large, closed by a strong flange of bone; zygomata relatively massive anteriorly, heavier than in *tickelli*; narial emargination wide, more or less U-shaped; soft palate (Fig. 2c) much as in *tickelli*; broad post-palatal spine; basioccipital pits a little deeper than in *tickelli*.

Baculum (Fig. 3c) long, with slender, cylindrical shaft, lacking any upward curvature or deflection, tip slightly thickened vertically, upper surface of shaft flattened proximally, the base widened to form paired basal flanges separated by a deep V-shaped aperture. The baculum is longer than in *H. tickelli* and differs in its lack of upward curvature and in narrower basal flanges which are more widely separated.

Inner upper incisor (i^2) relatively larger than in *H. tickelli*; outer upper incisor (i^3) more or less triangular in basal outline, intruded from the toothrow to lie directly behind i^2, its anterior face in contact with the posterior face of that tooth and lying behind a line joining the anterior faces of the canines (c^{1-1}), the tip of its roughly triangular base interposed between the postero-lateral face of i^2 and the antero-lateral face of c^1; centres of i^{3-3} lying on a line joining the centres of c^{1-1}, with i^2 and c^1 almost in contact labially. Remaining dentition much as in *tickelli* but third upper molar (m^3) a little further flattened and platelet-like, its second and third commissures more reduced; lower incisors (i_{1-3}) much imbricated, relatively more massive than in *tickelli*, i_2 with small posterior cingulum cusp behind central cusp, i_3 much thickened, with massive crown in which individual cusps are obscured but with prominent anterior and posterior cingulum cusps, its lateral diameter less than its diameter from front to back. In general, the dentition is considerably heavier than in *tickelli* (Pls 3d, f, 4f).

Measurements of *Hesperoptenus tomesi* are given in Tables 1 and 2.

DISTRIBUTION. MALAYA (Malacca; also two examples from an unknown Malayan locality); BORNEO (Sabah).

REMARKS. Davis (1962: 42) recorded as *Hesperoptenus doriae* a specimen from the Sapagaya Forest Reserve, Sandakan, Sabah, Borneo (5°37′N 118°04′E). Through the kindness of Dr J. C. Moore, lately of the Field Museum of Natural History, Chicago, I have been able to examine this specimen, now Field Museum 77025, collected by D. D. Davis on 29 July 1950. As Davis pointed out, it is a juvenile male, but is, however, much larger than the adult holotype of *doriae*, with length of forearm 42·8 mm and c–m^3 7·3 mm, and, although badly damaged with much of the cranium lost, the skull agrees closely with that of *tomesi* to which the specimen must be referred. It is thus the first of the species to be reported from

Borneo. The specimen differs slightly from the Malayan holotype of *tomesi* in the positional relationship of the upper incisors, the outer tooth (i^3) being a little less intruded from the toothrow, with the inner upper incisor (i^2) and the canine (c^1) separated by a slightly wider interspace. A brief account of this specimen can be found in Hill (1972 : 38).

Hesperoptenus tomesi is clearly separated from *H. tickelli* by differences in coloration, cranial architecture, baculum and dentition. That it represents a distinct species cannot be doubted, as Tate (1942 : 268) pointed out from a consideration of the anterior part of the orbit in *tickelli* and *tomesi*. The unique features of the species were first recognized by Tomes who has labelled the holotype '*V. dedalion* n. s.', a circumstance remarked by Thomas (1905 : 576) who would have used the name suggested by Tomes had it matched euphoniously with the generic epithet *Hesperoptenus.*

Hesperoptenus blanfordi (Dobson, 1877)

Vesperugo (*Hesperoptenus*) *blanfordi* Dobson, 1877 : 312. Tenasserim.

Vesperugo (*Hesperoptenus*) *blanfordi*, Dobson, 1878 : 242.

Vesperugo blanfordi, Anderson, 1881 : 133 ; Blanford, 1891 : 317.

Hesperoptenus blanfordi, Jentink, 1888 : 182 ; Trouessart, 1897 : 116 ; 1904 : 83 ; Miller, 1907 : 211 ; Kloss, 1908 : 158 ; Robinson & Kloss, 1915 : 116 ; Thomas, 1916 : 2 ; Wroughton, 1918 : 393 ; Gyldenstolpe, 1919 : 137 ; Chasen, 1940 : 52 ; Tate, 1942 : 270 ; Ellerman & Morrison-Scott, 1951 : 174 ; Medway, 1969 : 38 ; Hill, 1972 : 37 ; Hill & Thonglongya, 1972 : 191.

HOLOTYPE. Adult male No. 157a in the Indian Museum, Calcutta. In alcohol. Presented by W. T. Blanford.

TYPE LOCALITY. The holotype is said by Blanford (1891 : 318) to have been obtained east of Moulmein in Burma.

DIAGNOSIS. Much smaller than *H. tickelli* or *H. tomesi* ; internarial region densely haired ; tragus (Fig. 1e) less acutely pointed ; facial warts imperceptible; upper surface of forearm densely haired ; a broad, cushion-like pad at base of thumb ; braincase flattened ; postorbital region relatively much wider ; outer upper incisor (i^3) greatly reduced ; third molars (m $\frac{3}{3}$) more reduced.

DESCRIPTION. Muzzle very low, wide, moderately furred, nostrils semi-lunate, opening sublaterally, no perceptible grooves behind each nostril ; internarial region densely clothed with short hairs to lower edge of nostrils ; lower lip naked except for a few sparse hairs ; a prominent naked area beneath the symphysis menti preceding a low or almost imperceptible wart ; facial warts almost imperceptible or absent ; ear nearly subquadrate but rather more triangular than in *H. tickelli* or *H. tomesi*, its anterior margin strongly convex proximally, with well-developed, roundly pointed basal lobe, distally nearly straight to broadly rounded tip ; posterior margin of ear slightly convex in its distal third, its lower part similarly convex but with a shallow central concavity ; antitragal lobe thickened ; a low, barely perceptible wart, with a few longer hairs, just above the junction of the posterior margin of the ear with the side of the head ; outer surface of conch furred for about one third of its length, a few sparse hairs internally. Tragus (Fig. 1e) slightly hatchet-shaped, the inner margin sharply concave to a rounded, anteriorly directed tip, upper margin nearly horizontal, posterior margin straight or slightly convex, with a large triangular lobe at its base.

Thumb very short with strong claw, the upper surface of the thumb clothed with short hairs ; a broad, well-developed pad or cushion extending over the base of the thumb and of the second metacarpal ; third and fourth metacarpals usually subequal, fifth a little shorter ; upper surface of forearm densely clothed with fine, short hairs ; upper surface of tibia naked ; feet very small, the sole thickened, a few sparse hairs on the digits ; prominent, rounded post-calcarial lobe supported by a supplementary cartilaginous calcarial spur. No male example in alcohol is available but Dobson (1877 : 313) states that the penis of the holotype resembles that of *H. tickelli*. Dorsal surface bright chestnut brown, ventral surface similar in colour.

Skull (Pl. 4a–c) very small, braincase flattened, wide, with lambdoid ridges but no sagittal crest ; frontal region barely elevated, the cranial profile almost straight ; postorbital region wide, its width exceeding the width across the canines at the alveoli ; a trace only of supraorbital ridges ; slightly inflated lateral rostral swellings with small supraorbital tubercles ; a shallow median rostral depression ; narial emargination deep, extending posteriorly to a line joining the posterior margins of the anteorbital foramina, U-shaped ; anteorbital foramen large, enclosed by a narrow bar ; zygomata slender ; lower maxillary margin of orbit flange-like ; pre-palatal emargination wide anteriorly, its lateral margins extending beyond the inner faces of the inner upper incisors (i^{2-2}), the emargination extending posteriorly almost to a line joining the posterior faces of the canines (c^{1-1}) ; posterior edge of the emargination sometimes with a narrow tongue-like extension into the palate, on occasion extending as far as a line joining the mesostyles of the first upper molars (m^{1-1}). Soft palate (Fig. 2d) with six post-canine ridges, the first straight, unbroken, the second slightly curved, narrowly separated, remainder curved, medianly divided, the last small. Post-palatal extension short, wide, with prominent, broad post-palatal spine ; shallow basioccipital pits not excised sharply into the basisphenoid, separated by a broad ridge.

Upper incisive dentition similar to that of *H. tomesi* but outer incisor (i^3) very small, sometimes minute, one quarter or less the basal area of the inner tooth (i^2), with prominent cingulum and small central cusp, intruded to lie directly behind i^2, its anterior face in contact with the posterior face of that tooth, its outer face in contact with the inner face of the canine (c^1), i^2 and c^1 barely separated. Upper premolar (pm^4) not compressed in the toothrow, its length and width almost equal ; third upper molar (m^3) less than one half the crown area of first upper molar (m^1), with small metacone and much reduced second and third commissures ; lower incisors (i_{1-3}) linear, only slightly if at all imbricated, i_3 a little more massive than i_{1-2} ; anterior lower premolar (pm_2) small, its crown area about one quarter that of the second lower premolar (pm_4), rather compressed in the toothrow ; posterior triangle of third lower molar (m_3) much reduced, the hypoconid small, the entoconid almost obsolete, the posterior part of the tooth about one quarter to one third the area of the anterior triangle (Pl. 4a, c, g).

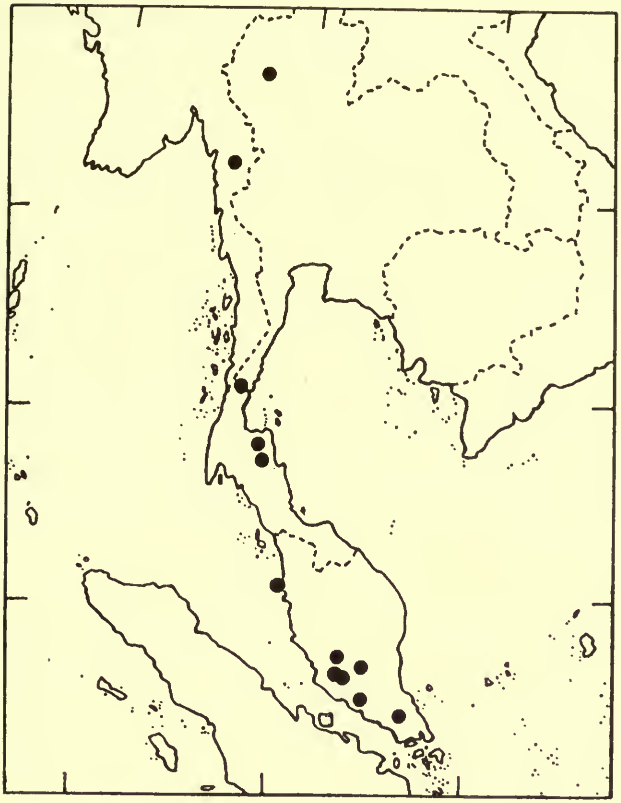

FIG. 5. *Hesperoptenus blanfordi*, distribution.

Measurements of *H. blanfordi* appear in Tables 1 and 2.

DISTRIBUTION (Fig. 5). BURMA (Dobson, 1877 : 312 ; 1878 : 242 ; Anderson, 1881 : 133 ; Blanford, 1891 : 318) ; THAILAND (Jentink, 1888 : 182 (Jongo Hills, perhaps = Chongo Hills, 10°17′N 99°01′E) ; Robinson & Kloss, 1915 : 116 ; Thomas, 1916 : 2 ; Gyldenstolpe, 1919 : 137 ; Hill & Thonglongya, 1972 : 191); MALAYA (Anderson, 1881 : 133 ; Blanford, 1891 : 318 ; Thomas, 1916 : 2 ; Hill, 1972 : 37).

REMARKS. Flattening and broadening of the braincase, with a wide postorbital region and rostrum, is characteristic of the vespertilionine genera *Tylonycteris* and *Mimetillus*, which also have pads on the thumbs and feet. In these, however, the braincase is yet more flattened than in *H. blanfordi* and no extensive shortening of the rostrum has occurred. Rostral inflation in *H. blanfordi* is of the same order as that in *Tylonycteris*, with the supraorbital area swollen to develop sometimes a small tubercle. In *Mimetillus* the whole of this area is inflated, together with the upper part of the bar enclosing the anteorbital foramen and the region immediately above this aperture, but with no definite tubercle. Although *Tylonycteris* and *Mimetillus* have the same dental formula as *Hesperoptenus*, the inner upper incisor (i^2) is bicuspid and the outer upper incisor (i^3) remains in the toothrow, separated from the canine by a small interspace. Further, in *Mimetillus* the wing is much reduced by shortening of the third and fifth digits ; in *H. blanfordi* the digits are not reduced and indeed are relatively rather long.

Of other vespertilionine bats with pads on thumbs and feet, *Eudiscopus denticulus* has an extreme degree of flattening of the skull with uninflated, unshortened, rostrum and retains the anteriormost upper premolar (pm^2) with a minute second lower premolar (pm_3) intruded between the anterior (pm_2) and posterior (pm_4) lower premolars. The braincase is higher in *Myotis rosseti* which has a caniniform outer upper incisor (i^3) exceeding the inner tooth (i^2) in basal area and which also retains the anteriormost upper premolar (pm^2) ; *Glischropus tylopus* cranially is like *Pipistrellus*, with the rostrum unexpanded and not much shortened although i^3 is extruded to lie alongside i^2, the four incisors forming a straight line, and with pm^2 present and retained in the toothrow. In all of these, i^2 remains rather elongate as it is in *Tylonycteris* and *Mimetillus*, and is similarly bicuspid. The massive, unicuspid i^2 and displaced i^3 ally *blanfordi* with *H. tickelli* and *H. tomesi* which it almost exactly resembles in the features of its upper incisive dentition although in a number of other features it differs quite sharply from either of these species.

RELATIONSHIPS

It is clear that *Hesperoptenus* as here understood embodies two rather widely separated trends, one represented by a single species (*doriae*), the other by three (*tickelli*, *tomesi* and *blanfordi*). At the same time, one species of the latter group (*blanfordi*) is quite sharply removed from its associates and apparently represents a further course of adaptation.

Thomas (1902 : 220) thought *Hesperoptenus* related to *Philetor* but apart from any other considerations the upper incisors of *Philetor* differ widely, the inner tooth (i^2) being elongate, long and bicuspid, with the outer tooth (i^3) not displaced. Indeed, *Philetor* is closely related to *Pipistrellus* (Hill, 1966 : 380 ; 1971 : 143). Miller (1907 : 211) compared the dentition of *Hesperoptenus* with *Eptesicus* and *Vespertilio* but examined only *tickelli*, and Tate (1942 : 232, 233, 268) included the genus among the 'pipistrelloid' genera. Tate added (p. 269) that in *tickelli* (he did not examine either *doriae* or *blanfordi*) the upper incisors show an interesting intermediate condition between the *Pipistrellus*-like genera which have mostly a bicuspid inner tooth (i^2), with the outer tooth (i^3) present, and the *Scotophilus*-like genera in which i^2 is unicuspid and i^3 is lost. In *doriae*, *tickelli*, *tomesi* and *blanfordi* i^2 is massive and unicuspid and in all but the first of these i^3 is markedly displaced inwardly from the toothrow, this feature reaching an extreme in *tomesi* and *blanfordi*. *Hesperoptenus doriae* indeed stands nearest to the pipistrelline genera and has a number of similarities to *Glauconycteris* and, to a lesser extent, to *Chalinolobus*. Its braincase is rather inflated, its rostrum not much shortened or broadened to the extent that it is in *tickelli*, *tomesi* or *blanfordi*, and its outer upper incisors are not greatly displaced as they are in its congeners. It is therefore considered the least modified member of *Hesperoptenus*.

The remaining species *tickelli*, *tomesi* and *blanfordi* in many ways approach the 'nycticeine' genera (Tate, 1942 : 280) allied to *Scotophilus*, and, indeed, in these the elongated braincase and greatly broadened rostrum are features strongly reminiscent of that genus or of *Scotomanes*. The large species *tickelli* and *tomesi* are similar to *Scotophilus* in the general appearance of the head and ears and also in the shape of the tragus, which is widened to some extent at its centre, rather than elongate and more or less spatulate as in the pipistrelline genera. In fact, the early authors referred *tickelli* to *Nycticejus* (in part = *Scotophilus*) and, on occasion, even relatively modern specimens referred by previous identifiers to *Hesperoptenus* have been found to be examples of *Scotophilus*.

The nycticeine genera are characterized among other features by the unicuspid inner upper incisor (i^2) and by the loss of the outer upper incisor (i^3) and of the small anteriormost upper premolar (pm^2) although at the base of their sequence a rudimentary i^3 is sometimes present in *Scotozous* which also retains pm^2 ; the latter tooth also occurs sometimes in *Scotoecus*. *Scotozous* has been thought to be pipistrelline rather than nycticeine (Tate, 1942 : 259) but, if the African *rueppellii* is excluded, then, as Tate (p. 260) postulated, the genus with its remaining Indian species *dormeri* is transitional between *Pipistrellus* and the nycticeine genera in which i^3 and pm^2 are lost. In *Hesperoptenus*, contrary to the usual nycticeine condition, i^3 is present and furthermore usually well developed. However, shortening of the rostrum has led to its intrusion from the toothrow in three of four species, and, as in most nycticeines, pm^2 has been lost. It is effectively further separated from *Scotophilus* by the lack of any distortion of the W-pattern of the first and second upper molars (m^{1-2}) and from *Scotomanes* by its less widely expanded rostrum, the anterior orbital margin not swollen or beaded (although the flange-like margin of *tomesi* tends towards this condition), and its lack of a pronounced rostral depression.

Hesperoptenus provides, therefore, a further example of a tendency apparent among some Vespertilionidae to shorten and broaden the rostrum with concomitant reduction of the dentition, in some by the loss of the outer upper incisor (i^3) with consequent enlargement of the inner upper incisor (i^2), the loss of the anterior upper premolar (pm^2), and some reduction of the third upper molar (m^3). The process has not progressed as far in *Hesperoptenus* as in the genera most modified in these respects and, indeed, has taken a different course, with the removal of i^3 from the toothrow rather than its loss. One species (*doriae*) remains relatively unmodified, and one (*blanfordi*) has clearly diverged rather widely with further modification of the skull and with the development of pads on the thumbs. The latter, however, occur quite independently in various sections of the Vespertilioninae, in the 'myotine' type in *Eudiscopus* and *Myotis*, the 'pipistrelline' type in *Glischropus*, *Tylonycteris* and *Mimetillus*, and in *blanfordi* in a species that in many ways approaches the 'nycticeine' type. The conclusion seems unavoidable that *Hesperoptenus* must be placed with the genera *Scotozous*, *Scotoecus* and *Nycticeius* that link the more truly pipistrelline bats to the more modified, extreme nycticeine bats such as *Scotomanes* and *Scotophilus*.

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PLATE 1

Hesperoptenus doriae, holotype, Genoa Museum CE 40094, ♂, Sarawak. Ear and tragus. Skull, approx. × 4; lingual aspect of mandible, approx. × 5·5.

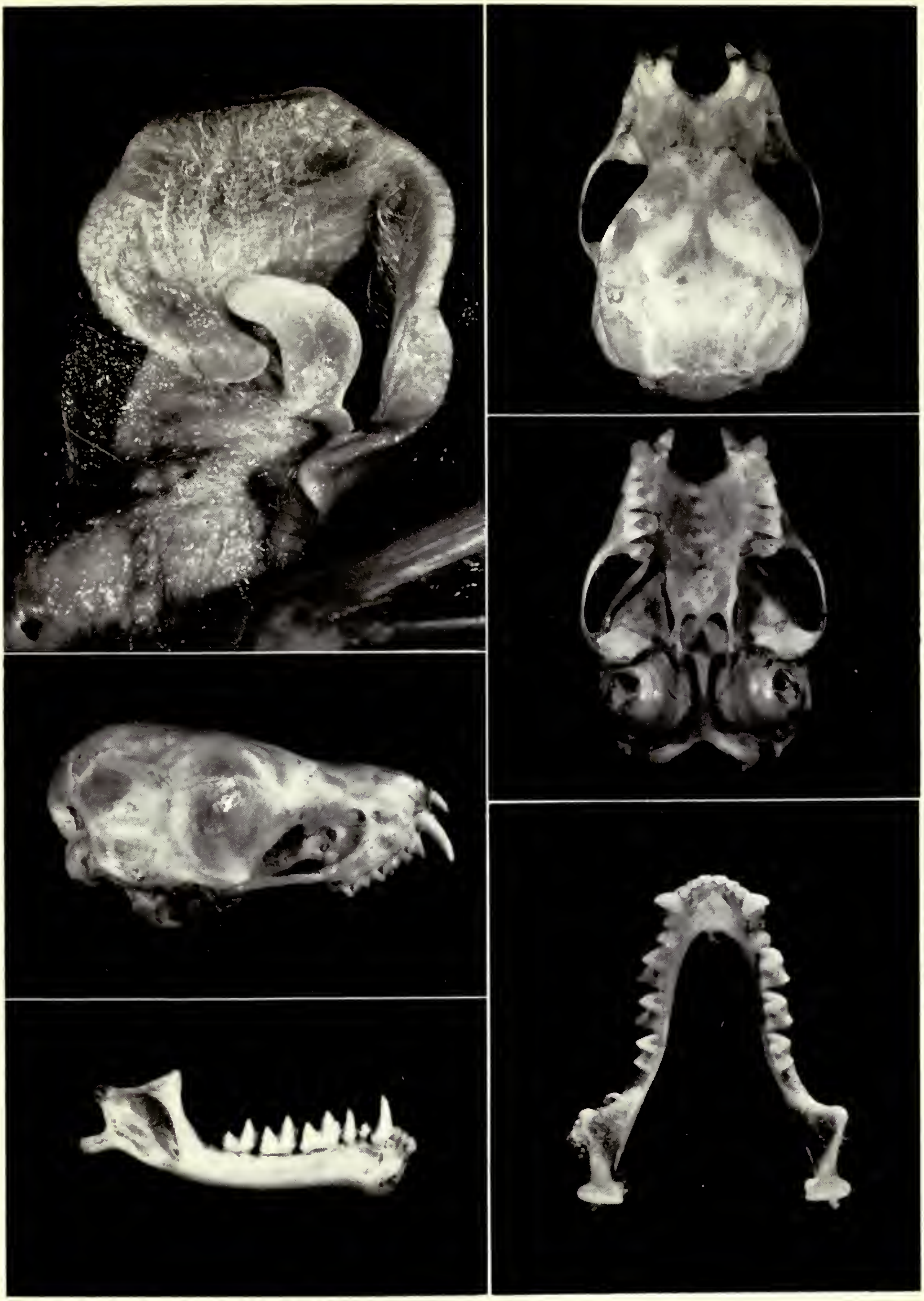


PLATE 2

Hesperoptenus doriae, holotype, Genoa Museum CE 40094, ♂, Sarawak. Dentition.

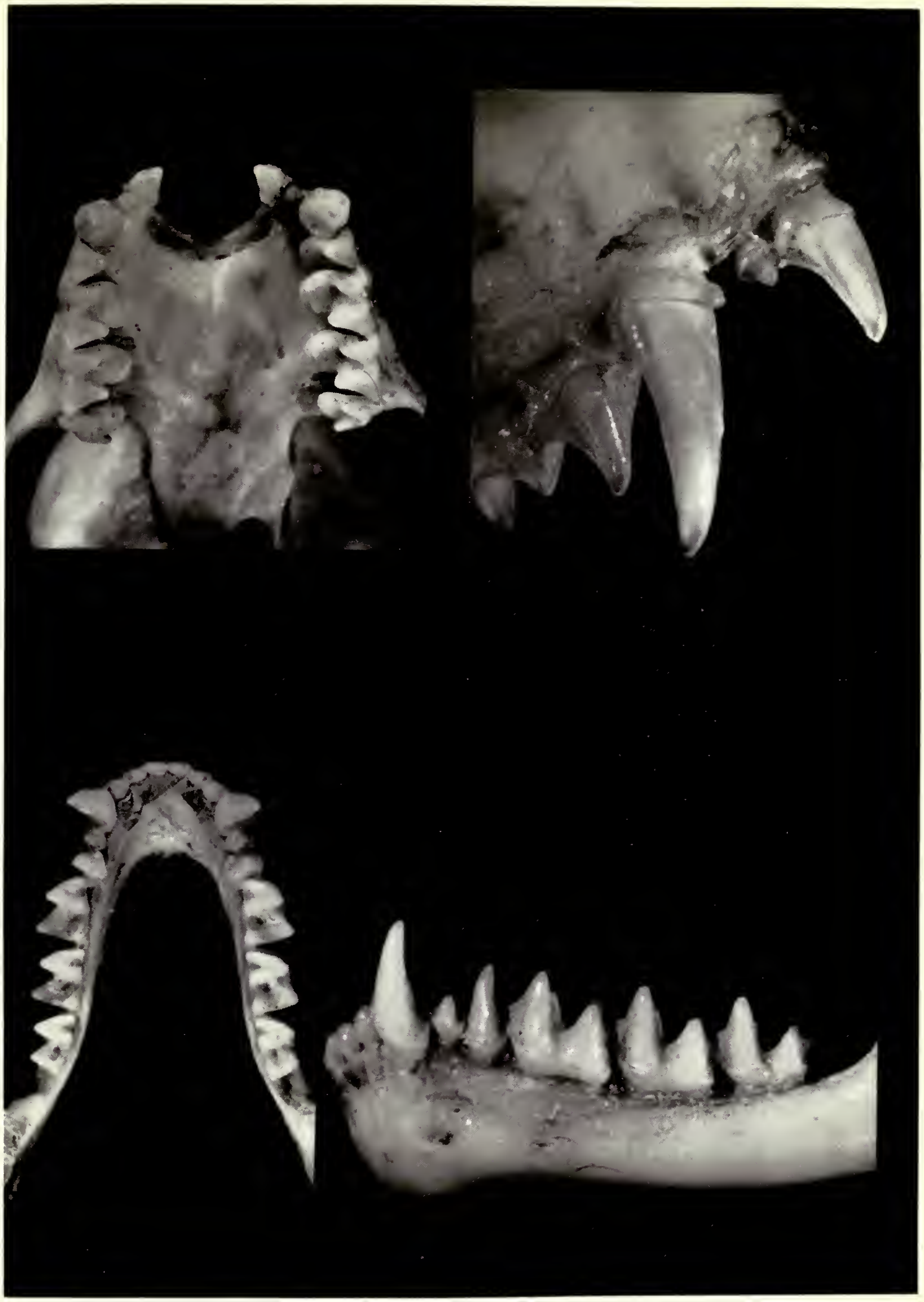


PLATE 3

Skull of: (a–c) *Hesperoptenus tickelli*, BM 12.11.28.46, ♀, India, approx. × 2; (d–f) *H. tomesi*, holotype, BM 7.1.1.428, ♂, Malaya, approx. × 2.

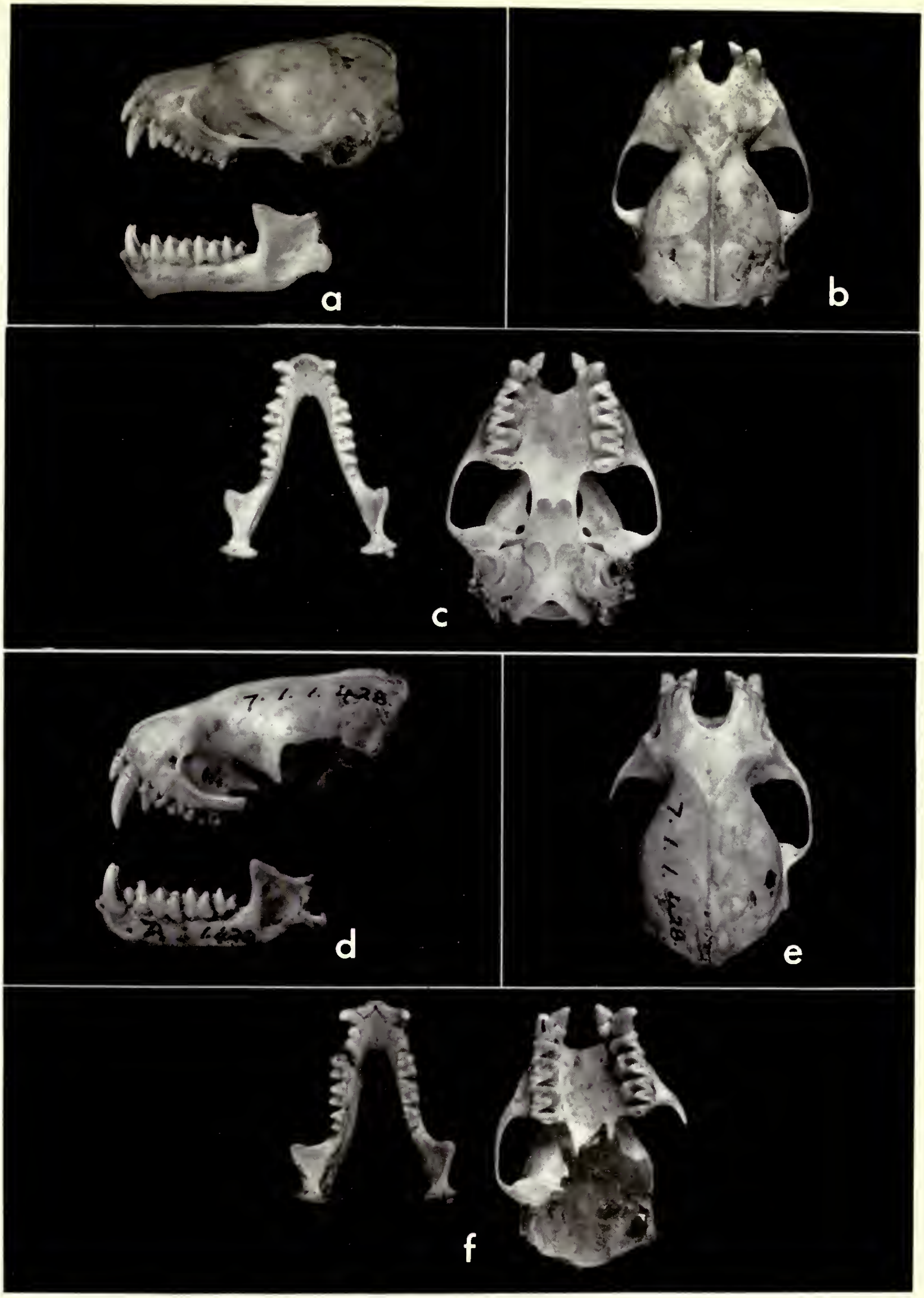
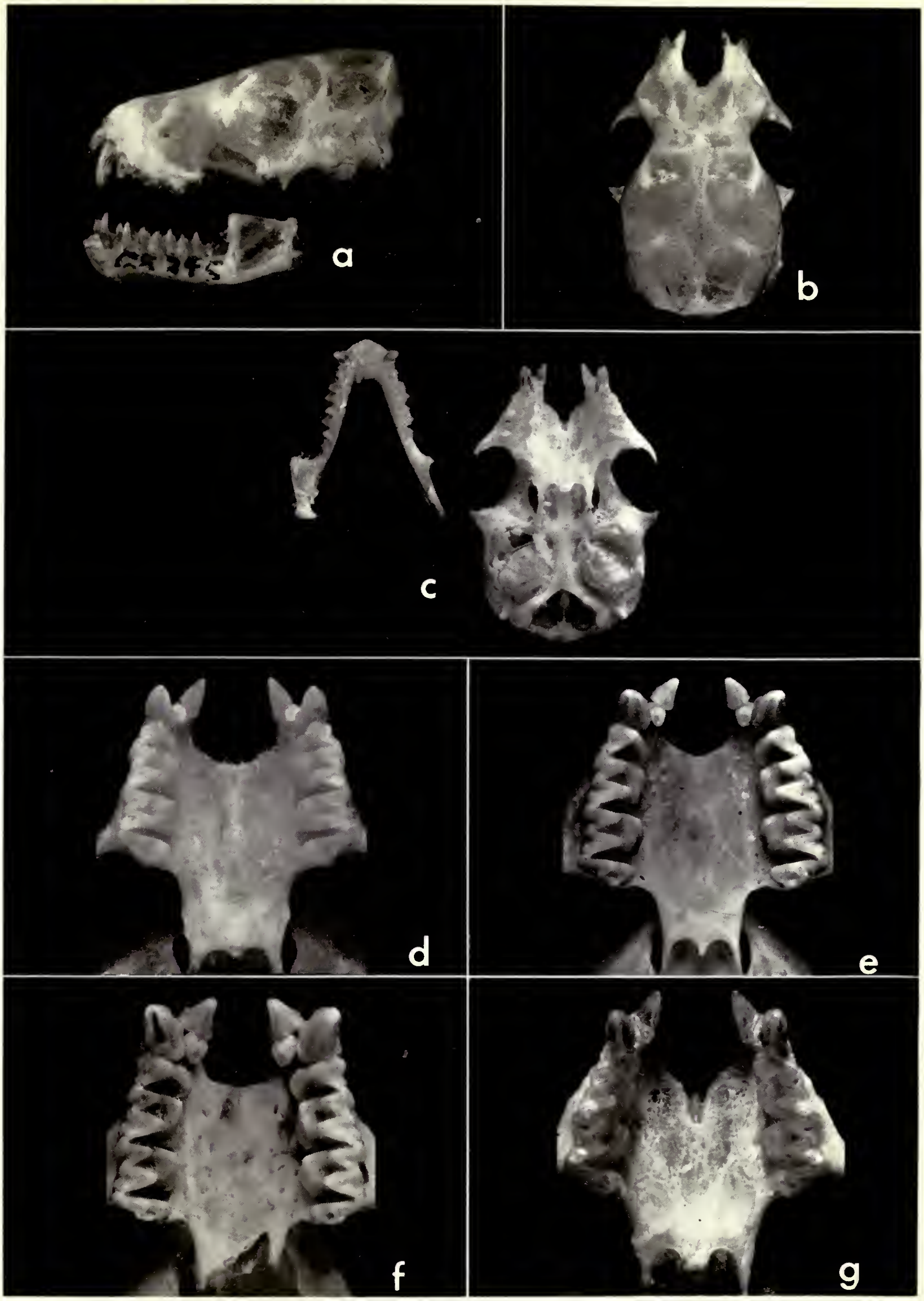

a
b
c
7.1.1.428.
d
7.1.1.428.
e
f

PLATE 4

Skull of: (a–c) *Hesperoptenus blanfordi*, BM 65.345, ♀, Malaya, approx. ×3. Maxillary dentition of: (d) *H. doriae*, BM 75.1873, ♀, Malaya, approx. ×5·5; (e) *H. tickelli*, BM 12.11.28.46, approx. ×3·5; (f) *H. tomesi*, holotype, BM 7.1.1.428, approx. ×4; (g) *H. blanfordi*, BM 65.345, approx. ×6·5.

PLATE 4



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TAXONOMY AND DISTRIBUTION OF THE *METAPHERETIMA ELONGATA* SPECIES-COMPLEX OF INDO-AUSTRALASIAN EARTHWORMS (MEGASCOLECIDAE : OLIGOCHAETA)

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TAXONOMY AND DISTRIBUTION OF THE *METAPHERETIMA ELONGATA* SPECIES-COMPLEX OF INDO-AUSTRALASIAN EARTHWORMS (MEGASCOLECIDAE : OLIGOCHAETA)

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By E. G. EASTON

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SYNOPSIS

Following studies on the setal and spermathecal systems of the *Metapheretima elongata* species-complex five species, *elongata*, *everetti*, *kinabaluensis*, *phacellotheca* and *stelleri* are recognized. The taxonomy and indigenous distributions of each are described.

INTRODUCTION

DURING their numerical revision of the oriental earthworm genus *Pheretima* auct. Sims & Easton (1972 : 252) proposed that the Indo-Australasian earthworm *Metapheretima elongata* (Perrier, 1872) and its allies should be recognized as a single species-complex. They assigned eighteen nominal species and subspecies to the complex and tabulated the variation in expression of several characters. The lack of obvious correlations, however, prevented the delineation of discrete groups of taxa from among the relatively short series of material which they examined.

Subsequently more detailed investigations have continued into the taxonomy of the acaecate members of the *Pheretima* group of genera (*Archipheretima*, *Ephemitra*, *Metapheretima* and *Planapheretima*) and in particular into the members of the *Metapheretima elongata* species-complex which have received special scrutiny. During this latter study the material was located on which many of the taxa and records of the *elongata* species-complex were based. Additionally material of the species *Metapheretima phacellotheca* (not previously included in the *elongata* group of species) was also examined from which it was concluded that this species too is closely allied to the complex. Recent additions to the collections of the British Museum (Natural History) also included many examples of the species-complex. Examination of all this material has provided the data presented in this report from which it is possible to recognize five species and to establish the indigenous distributions of each.

METHODS

During revision of the genus *Metapheretima* it became evident that discrete taxonomic assemblages could be recognized in the *elongata* species-complex on the expression of three characters :

1. The volume of a single segment. This value is derived from measurements of the diameter and length of the segment. In specimens that have been dissected the circumference is measured instead of the diameter. For convenience during the study, the segment selected for measurement was *vii* since the volume determination could be assessed when making the setal count (see below) so that a direct correlation could be established between segmental volume and setal number.
2. Number of setae. During preliminary studies it was observed that the setal number of *vii*, in addition to being easier to determine, was also less variable than that of *xx*, the other segment sometimes selected for study.
3. Number of spermathecae. The spermathecae of members of the *elongata* species-complex, although occasionally absent, are usually arranged in paired, ventrolateral batteries of up to 28 spermathecae, opening into intersegmental furrows 5/6 and/or 6/7. The number of pores in each spermathecal battery was recorded.

The three characters employed here as taxonomic criteria differ somewhat from those utilized by Sims & Easton (1972 : 256). These authors used the length of an individual as an expression of size since this value was readily available in published descriptions. During the present study it became evident that segmental volume provided a more accurate indication of size owing to the vicissitudes of relaxation and fixing techniques causing wide fluctuations in overall length in similarly proportioned individuals. Initially segment number was also employed in this study but the large proportion of the specimens available for examination proscribed by damage or regeneration caused the data to lack significance. Some authors (Beddard & Fedarb, 1895 ; Michaelsen, 1899, 1922) considered the number of segments bearing genital markings to be of taxonomic importance for distinguishing the species of the *elongata* species-complex. However, when this character was assessed and correlated with the other results the degree of overlap of the groups made it impractical to utilize it as a taxonomic criterion although several groups of individuals could be recognized which were related to those established using the criteria discussed above.

The majority of the taxa included within the *elongata* species-complex by Sims & Easton (1972) are known only from one or two series and whenever possible all the members of those series were examined in this study. Only in the cases of the common forms *biserialis* and *elongata*, often recorded from outside the *Pheretima* domain, were the number of specimens examined restricted by sampling. These two forms are usually considered synonymous and Sims & Easton (1972 : 256) suggested that they originated probably in the area bounded by Sumatra, Philippines, Celebes and Java. They concluded that all other records were the result of introduction. Gates (1972 : 182) however was of the opinion that these forms had originated in a smaller area : Borneo, Celebes and Philippines. All the records that could be traced from these areas were included in the study as well as a selection from several new series collected recently in Bali, Lombok, Sumbawa and Komodo. For many years *phacellotheca* has been known only from the type-series which is now unsuitable for study. It was found however that two specimens from Buru identified by Michaelsen (1934a) as *stelleri bonensis* so closely resembled the original description of *phacellotheca* as to require re-identifying with the result that they were included in the study as representatives of this species.

RESULTS

Correlation between each pair of characters was studied separately.

1. *Setal number : segmental volume.* The relationship between setal numbers and the volume of segment *vii* was tested (Fig. 1) and found to provide a means of

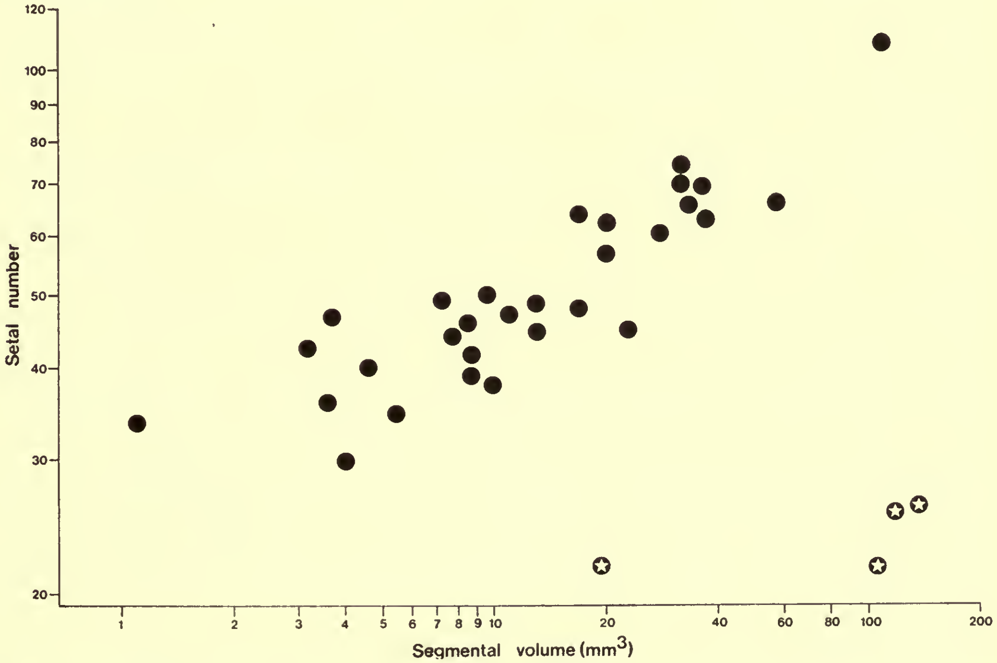

FIG. 1. Relationship between the setal number and segmental volume of segment *vii* (scales logarithmic). Origins of material : ✪ Mt Kinabalu (above 2100 m) ; ● other localities.

recognizing two distinct groups of individuals. The smaller cluster (depicted by circular symbols with star-shaped centres) includes only examples from the upper slopes of Mt Kinabalu, Sabah (*series A:* Sims & Easton, 1972 : 253), while the larger cluster (depicted by solid circular symbols) contains examples from all other parts of the *elongata* species-complex range. Examples from the larger cluster have considerably higher setal numbers for a given segmental volume than those of the smaller cluster. Examination of the other individuals from the samples identified as *series A* revealed that the majority of them belong to the smaller cluster.

In both groups there is a positive correlation between setal number and segmental volume. The size of an individual, and therefore the segmental volume, increases during an individual's life and it may be deduced from Fig. 1 that the number of setae also increases. This conclusion has a wide significance in view of the diagnostic value usually attributed to setal number. It is implicit from the literature that the setal number of a segment is assumed to remain fairly constant (allowing for loss, etc.) throughout the life of an individual ; indeed, many of the 'species' in the *Pheretima*-complex have been distinguished by smaller differences in the setal numbers than are recorded here.

2. *Anterior spermathecal batteries : posterior spermathecal batteries.* In the specimens studied each spermathecal battery of an individual rarely contained an identical number of pores although the discrepancies occurring between the right and left batteries within a furrow were small and apparently haphazard. The relationship between the mean number of spermathecae in a battery in furrow 5/6 and in 6/7 was tested (Fig. 2). A positive correlation was established between the sizes of the anterior and posterior batteries for most of the specimens with the posterior pair containing, on average, 20% more spermathecal pores than the anterior pair.

Two specimens, both from Buru (depicted by star-shaped symbols), depart significantly from the general trend. Both these specimens lack spermathecal batteries in furrow 6/7 (confirmed by internal examination) although there are large anterior batteries. Some of the other specimens also lacked posterior spermathecal batteries, but in all these individuals the anterior spermathecal batteries were very small or absent.

Some signs of clustering may be detected in the larger group of specimens, i.e. those with the usual spermathecal arrangement. Specimens from Sumbawa and Komodo (solid square symbols) and Lombok (open square symbols) have small spermathecal batteries, individuals from Borneo (solid circular symbols) and Celebes (open triangular symbols) have batteries of intermediate size while those from Balabac Island (open circular symbols) and Sangihe (solid triangular symbols) have large spermathecal batteries. The individuals from Mt Kinabalu (noted in Fig. 1 because of their low setal numbers) were indistinguishable from other specimens from Borneo.

3. *Setal number : size of spermathecal batteries.* Because of the strong positive correlation noted between the relative sizes of the anterior and posterior spermathecal batteries in the main cluster in Fig. 2 the regression line of the main cluster has been utilized as an axis in Fig. 3. Since this line passes close to the origin of

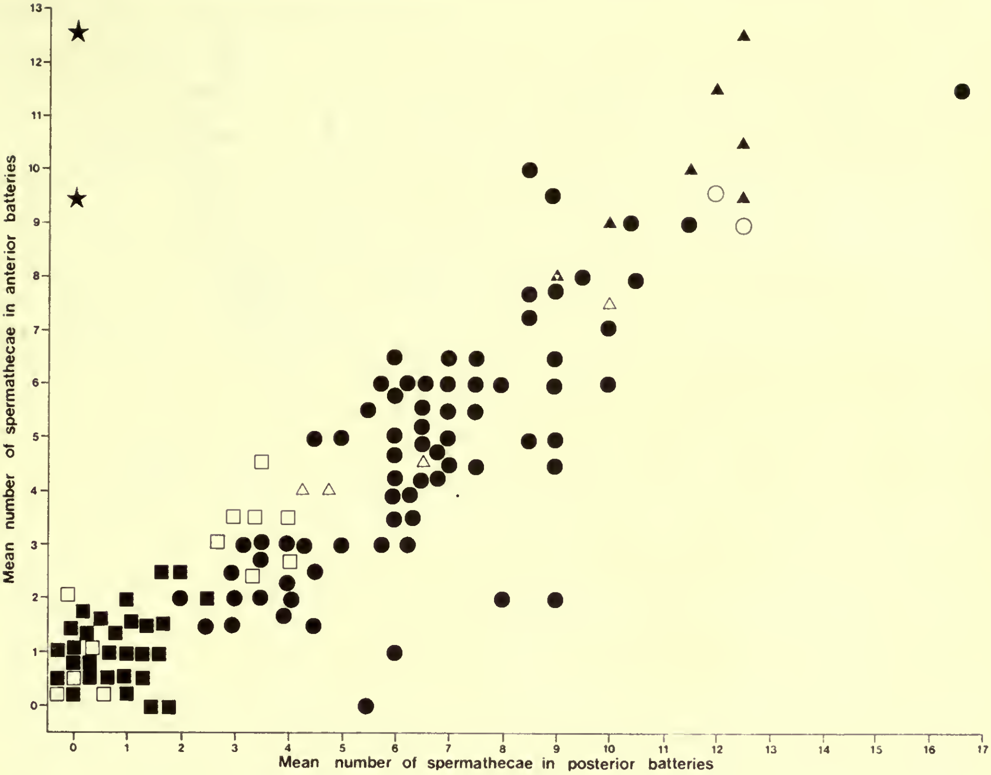

FIG. 2. Relationship between the mean number of spermathecae in the anterior (5/6) and posterior (6/7) batteries. Origins of material: ■ Sumbawa and Komodo; ☐ Lombok; ● Borneo; ○ Balabac Island; ▲ Sangihe; ◬ Kepulaud Taulaud; △ Celebes; ★ Buru.

Fig. 2 the positions of specimens along this axis are determined by the distance each occurs from the origin. (The positions of specimens along this axis may be calculated directly from the formula $x = \sqrt{(a^2 + b^2)}$, where a and b are the mean sizes of the anterior and posterior spermathecal batteries.) To facilitate the recognition of clusters, members of each sample are linked.

Most of the specimens plotted in Fig. 3 form two discrete clusters. The remaining individuals are scattered in an area, peripheral to the larger of these clusters, which is characterized by large spermathecal batteries and low setal numbers. The first cluster, characterized by high setal numbers and small spermathecal batteries, contains all of the specimens from Java, Bali, Sumbawa and Komodo (depicted by solid square symbols). The series from which these specimens were selected were remarkable in the high proportion of athecate individuals present: approximately half the clitellate portion of each series lacked spermathecae and therefore had to be excluded from this figure. Setal numbers of athecate individuals agreed closely with the thecate individuals plotted. The second cluster, containing individuals

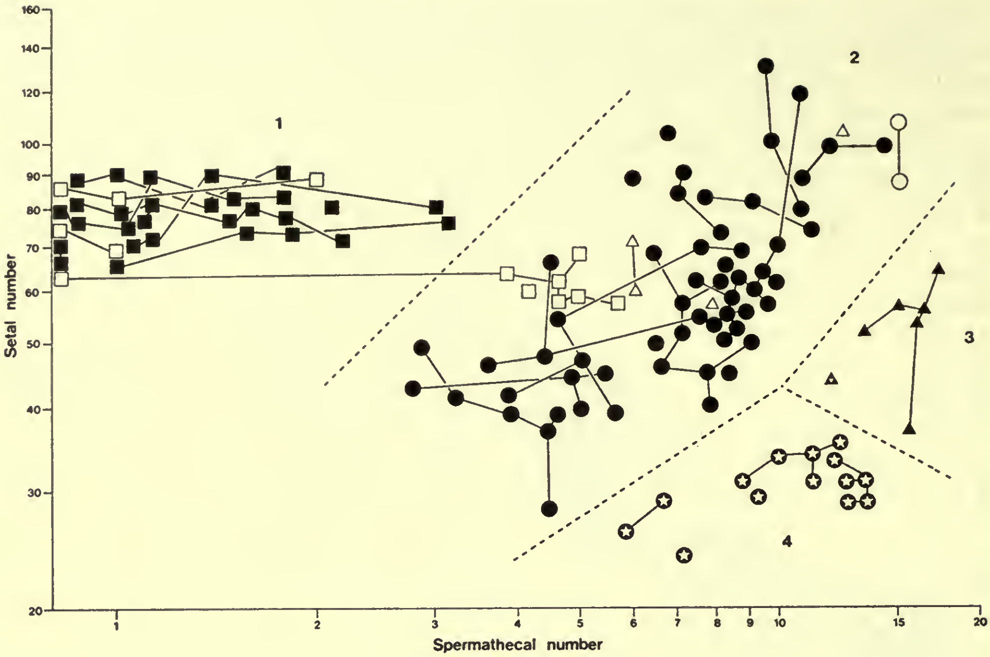

FIG. 3. Relationship between the setal number of segment *vii* and the spermathecal number, $\sqrt{(a^2+b^2)}$ (scales logarithmic). Members of each series are linked. Origins of material: ■ Sumbawa, Komodo, Bali and Java; □ Lombok; ● Borneo (individuals with a high setae : volume ratio); ✪ Borneo (individuals with a low setae : volume ratio); ○ Balabac Island; ▲ Sangihe; ◭ Kepulaud Taulaud; △ Celebes.

with a greater range of setal numbers and larger spermathecal batteries, includes all of the specimens from Balabac Island (open circular symbols), Celebes (open triangular symbols) and Borneo (solid circular symbols) with the exception of the individuals from Mt Kinabalu (circular symbols with star-shaped centres) which were noted (F1) for their low setal numbers.

Specimens from Lombok (open square symbols) occur in both clusters. Individuals from low altitudes (*c.* 50 m) however belong to cluster 1 while, with one exception, those from high altitudes (*c.* 400 m) belong to cluster 2.

The specimens situated peripherally to cluster 2 are those from Sangihe (solid triangular symbols), Kepulaud Taulaud (partially filled triangular symbols) and Mt Kinabalu (circular symbols with star-shaped centres). Since these may be distinguished by the difference in their setal development it is considered that two further clusters should be recognized among material from this area; one containing the specimens from Sangihe and Kepulaud Taullaud(cluster 3) and the other the Mt Kinabalu specimens (cluster4). Although the individuals of cluster 4 resemble those of cluster 3 in their relationships between setal and spermathecal development, it should be recalled (Fig. 1) that the setal development, compared with the segmental volume, is reduced in members of cluster 4, while the relationship of the segmental volume to the spermathecal development in individuals in this cluster is closer to that found in cluster 2.

The two specimens from Buru (depicted by star-shaped symbols in Fig. 2) have not been plotted in Fig. 3 since they did not occur in the main cluster in Fig. 2. They most closely resemble specimens from Sangihe and Kepulaud Taulaud (cluster 3) on setal numbers and the size of the anterior spermathecal batteries.

The marker attributes of the five groups of individuals recognized above have been tabulated in Table 1. Morphologically groups 1, 2 and 3 form a series in which the only differences noted are increases in the sizes of spermathecal batteries in individuals of a similar size. Group 4 resembles group 2 but has lower setal numbers. Group 5 differs from group 3 only in lacking spermathecal batteries in furrow 6/7.

TABLE 1

Marker attributes of the morphological groups

Group	Setae : segmental volume (Fig. 1)	Positions of spermathecal pores (Fig. 2)	Size of spermathecal batteries (Fig. 3)
1. (*elongata*)	high	5/6 and 6/7	small (cluster 1)
2. (*everetti*)	high	5/6 and 6/7	intermediate (cluster 2)
3. (*stelleri*)	high	5/6 and 6/7	large (cluster 3)
4. (*kinabaluensis*)	low	5/6 and 6/7	intermediate* (cluster 4)
5. (*phacellotheca*)	high	5/6 only	large

* See text.

NOMENCLATURAL CONSIDERATIONS

The type-series of nine of the eighteen nominal species and subspecies assigned to the *elongata* species-complex were examined during the preparation of this report, thus permitting these names to be readily allocated to the appropriate morphological group. The types of *elongata* Perrier, 1872 and *biserialis* Perrier, 1875 were not examined, but Michaelsen (1910c) had previously synonymized the taxa and there is no evidence to dispute this decision. On the basis of Michaelsen's published description, as well as those of more recent workers (Stephenson, 1923; Gates, 1972) the types as well as the majority of records of both *elongata* and *biserialis* can be assigned to group 1 as also may one other taxon, *acystis* Beddard, 1895.

Although the type-series of seven other taxa could not be located during the preparation of this report, it is possible to estimate approximate co-ordinates in Figs 1, 2 and 3 for each of the taxa from the original descriptions. None of the original descriptions recorded segmental volume but approximate values have been calculated based on the mean segmental lengths (total length/segment number) and the maximum diameters. The estimated co-ordinates and the group to which each taxon is assigned are shown in Table 2 where data regarding *stelleri everetti*: Michaelsen, 1899 are also recorded.

In Table 2 it is uncertain to which group *kinabaluensis* Beddard & Fedarb, 1895 should be assigned. The original description lacks any data regarding setal numbers

TABLE 2

Estimated co-ordinates based on published data

Taxon	Segmental volume (mm³)	Setal number on *vii*	Positions of spermathecal batteries	Size of spermathecal batteries	Group
baritoensis	11.5	49	5/6/7	4·7	2
beranensis beranensis	1·1	47	5/6/7	8·1	2
kinabaluensis	47·7	–	5/6/7	10·1	2, 3 or 4
phacellotheca	14·2	46	5/6	—*	5
stelleri annectens	28·8	40	5/6/7	26	3
stelleri bonensis	95·4	131	5/6/7	31	2
stelleri everetti (sensu Michaelsen, 1899)	126·2	85	5/6/7	28	3
stelleri koroensis	176·6	60	5/6/7	8	2

* Size of spermathecal batteries not recorded.

so it could belong to any of groups 2, 3 or 4. It seems unlikely to belong to group 3 because the type locality of *kinabaluensis* is Tamburungare, Mt Kinabalu, Sabah, at an altitude of 2350 m (7700 ft) and only groups 2 and 4 are known from Borneo. It is however proposed to assign *kinabaluensis* to group 4 since it is evident from Sims & Easton (1972) that group 4 (*series A*) is the commonest form at altitudes of more than 2100 m.

Information on three records from the Borneo–Celebes area, *stelleri* : Michaelsen, 1896 : 202 ; *stelleri* (*typica*) : Ude, 1932 : 155 and *elongata* : Ude, 1932 : 155, lacks sufficient detail to establish even approximate co-ordinates for this material. Nevertheless, as the two records of *stelleri* are from Borneo at altitudes at which group 2 is believed to be the only representative of the complex present, both are assigned to that group, while the record of *elongata*, from south Celebes, is allocated to group 1. Although all other records from Celebes have been assigned to groups 2, 3 or 5, they are from the north and west which are ecologically distinct from the south which resembles Lombok and Sumbawa where group 1 is indigenous (see Distribution).

Each morphological group may be recognized as forming a distinct taxonomic unit. The status of each and its relationships with the others still require considerable study but since there is no evidence of hybridization, although several samples studied contain representatives of more than one group, it is proposed to consider each as a distinct species while retaining them within the *elongata* species-complex. The senior synonym allocated to each group is given in Table 1.

TAXONOMY

Metapheretima elongata species-complex

Metapheretima elongata species-complex : Sims & Easton, 1972 : 252.
Metapheretima phacellotheca : Sims & Easton, 1972 : 233.

Diagnosis. *Metapheretima* with male pores within copulatory pouches lacking stalked glands. Spermathecae in paired, ventrolateral batteries opening in intersegmental furrows 5/6 and/or 6/7. Genital markings simple, large, paired, presetal, on *xix* and successive segments in line with or slightly ventral to the male pores.

Description. *External characters.* Length 40–360 mm, diameter 1·5–10 mm. 100–220 segments. Clitellum *xiv–xvi.* First dorsal pore 12/13. Setae regularly distributed around each segment, 20–130 on *vii*, 36–86 on *xx*; setal distance *aa* = 1–2*ab*; occasionally setae *a* and *b* enlarged.

Male pores paired on short penes within shallow copulatory pouches on *xviii*, *c.* 0·25 body circumference apart. Female pore single; midventral *xiv.* Spermathecal pores small, numerous, arranged in paired, ventrolateral batteries each comprising up to 28 pores, intersegmental in 5/6 and/or 6/7.

Genital markings (Fig. 5a): paired, simple, large, oval presetal papillae on *xix* and successive segments in line with or slightly ventral to the male pores; occasionally present on *vi*, *vii* and *xvii.*

Internal characters. Septa 4/5–7/8 thickened, 8/9 membranous, 9/10 absent, 10/11–13/14 thickened. Intestine begins in *xv.* Lateral hearts in *x*, *xi*, *xii*, usually *xiii.*

Holandric; testes sacs large, paired, extending to the dorsal line in *x* and *xi*; seminal vesicles paired in *xi* and *xii*, the anterior pair enclosed in the posterior testes sacs. Coelomic sacs in *xiii*, *xiv.* Spermathecae (Fig. 5b) numerous, in paired batteries of up to 28 in *vi* and/or *vii.* Copulatory pouches shallow, confined to the body wall of *xviii.*

Distribution. Indigenous records: Kepulaud Taulaud; Sangihe; Celebes; Buru; Balabac Island, Palawan; Borneo; ? Madura; east Java; Bali; Lombok; Sumbawa; Komodo; ? Gt Bastard Island, Flores.

Four of the five species included in this species-complex are known only from the indigenous range. The fifth, *elongata*, has been introduced into many parts of the world.

Remarks. This species-complex is readily recognized by the positions of the spermathecal pores and the form of the male pores. Three other species of *Metapheretima* with similar features may be distinguished either by the absence of genital markings in the case of *M. annamanensis*, a bithecal species known only from the Lang Biang Peaks, Vietnam, or by the form of the genital markings in the cases of *aringeana* from Kelantan, Malaya, and *grata* from New Guinea. In *aringeana* the postclitellar genital markings are paired and occur only on *xvii* and *xix* as circular pads with many small pores while in *grata* they are small and numerous, being present only in the region of the spermathecal pores. This latter species also has stalked glands discharging into the copulatory pouches which are large and invade the coelom. Clitellate individuals from the indigenous range of the species-complex are rarely athecate but the majority of specimens examined from introduced populations lack spermathecae. In these populations athecate individuals may be identified by the arrangement of the genital markings and the form of the copulatory pouch. Outside of the *Pheretima* domain, identification is easier since only one

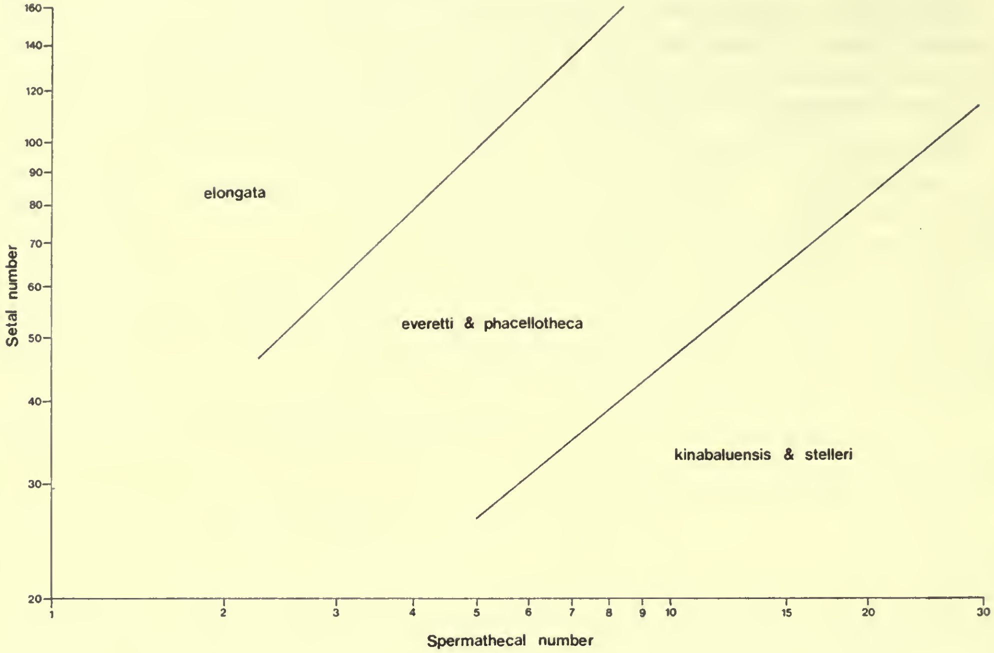

FIG. 4. *Metapheretima elongata* species-complex. Relationship between the setal number of segment *vii* and the spermathecal number, $\sqrt{(a^2+b^2)}$, for the member species.

other species of *Metapheretima* is commonly encountered. This species, *M. taprobanae,* has paired spermathecal pores in furrow 7/8 and genital markings on *vi–ix* and *xviii–xxii*. Additionally it is considerably smaller than the members of the *elongata* species-complex, rarely exceeding 140 mm in length.

The species of the *elongata* species-complex may be distinguished from one another by comparison of the setal number on *vii* and the size of the spermathecal batteries (Fig. 4). (The size of the spermathecal batteries is calculated by substituting the mean size of anterior and posterior spermathecal batteries of an individual for a and b in the formula $x = \sqrt{(a^2 + b^2)}$.)

Two pairs of species, *everetti–phacellotheca* and *stelleri–kinabaluensis,* need additional characters to be assessed for differentiation. In the first pair, *M. everetti* has spermathecae in furrows 5/6 and 6/7 while *phacellotheca* has spermathecae in furrow 5/6 only. In the second, *M. stelleri* has very numerous setae on *vii* (up to 130) while *kinabaluensis* has few setae (less than 40).

Metapheretima elongata (Perrier, 1872)

Perichaeta elongata Perrier, 1872 : 124 ; Beddard, 1895 : 431.
Megascolex elongata : Vaillant, 1889 : 81.
Amynthas elongatus : Beddard, 1900 : 650.
Pheretima elongata : Michaelsen, 1900 : 265 ; Cognetti, 1905a : 33 ; Michaelsen, 1910a : 252 ; (= *biserialis*) Michaelsen, 1910c : 84 ; Michaelsen, 1913 : 262 ; Michaelsen, 1920 : 68 ;

Stephenson, 1920 : 222 ; Michaelsen, 1922 : 32 ; Stephenson, 1922 : 433 ; Stephenson, 1923 : 298 ; Stephenson, 1924 : 339 ; Gates, 1926a : 208 ; Gates, 1926b : 444 ; Gates, 1926c : 183 ; Gates, 1926d : 153 ; Stephenson, 1926 : 256 ; Stephenson, 1929 : 237 ; Gates, 1930 : 309 ; Gates, 1931 : 378 ; Stephenson, 1931 : 58 ; Gates, 1932 : 391 ; Gates, 1933 : 525 ; Cernosvitov, 1934 : 49 ; Cernosvitov, 1935 : 11 ; Gates, 1936 : 413 ; Gates, 1937a : 318 ; Gates, 1937b : 352 ; Gates, 1937c : 201 ; Gates, 1939 : 87 ; Daweini, 1940 : 110 ; Gates, 1954 : 86 ; Gates, 1959 : 9 ; Gates, 1960a : 57 ; Gates, 1960b : 256 ; Gates, 1961a : 62 ; Gates, 1961b : 308 ; Gates, 1972 : 182 ; [non Ohfuchi, 1956 : 148 (= *Amynthas morrisi*)].

Pheretima (*Pheretima*) *elongata* : ? Ude, 1932 : 155 ; Michaelsen, 1934a : 108.

Perichaeta biserialis Perrier, 1875 : 1044 ; Beddard, 1890 : 63 ; Beddard, 1895 : 430 ; Michaelsen, 1897 : 226 ; (= *acystis*) Horst, 1899 : 202 ; Beddard & Fedarb, 1899 : 803.

Megascolex (*Perriera*) *biserialis* : Vaillant, 1889 : 76.

Amynthas biserialis : Michaelsen, 1899 : 21 ; Beddard, 1900 : 638.

Pheretima biserialis : Michaelsen, 1900 : 256 ; Michaelsen, 1902 : 9 ; Michaelsen, 1904 : 285 ; Cognetti, 1905a : 30 ; Cognetti, 1905b : 2 ; Ude, 1905 : 471 ; Michaelsen, 1907 : 44 ; Michaelsen, 1908a : 187 ; Michaelsen, 1908b : 14 ; Ohfuchi, 1940 : 13 ; Ohfuchi, 1956 : 151.

Perichaeta acystis [nom. nov. pro *biserialis* : Beddard, 1890 (non Perrier, 1872)] Beddard, 1895 : 423.

Perichaeta monocystis (lapsus pro *acystis*) Horst, 1899 : 202.

Metapheretima elongata species-complex : Sims & Easton, 1972 : 256, footnote 1.

Metapheretima elongata : Jamieson (in press).

TYPE LOCALITY. Peru.

DIAGNOSIS. *M. elongata* species complex with numerous setae (usually about 80 on *vii* but up to 130 on large individuals) and small spermathecal batteries (rarely more than 3 spermathecae in a battery) in furrows 5/6/7, or 5/6 or 6/7 only or absent. Spermathecal batteries usually present in about 50% of the clitellate portion of indigenous populations to about only 15% of the clitellate portion of introduced populations.

DISTRIBUTION. *Indigenous records* (Fig. 6). ? Madura ; east Java ; Bali ; Lombok ; Sumbawa ; Komodo ; ? Gt Bastard Island, Flores ; ? south-east Celebes. The establishment of the indigenous range of this species is discussed below (see Distribution). The specimens identified from Bali, Lombok, Sumbawa and Komodo represent new indigenous records for the species.

Introduced records. This species has been introduced into many parts of the world ; for a summary of these records see Gates (1972). During the preparation of this paper specimens from Queensland, Australia ; Tahiti ; Antigua, West Indies ; and Oman were identified. These represent new introduced records for the species.

Metapheretima everetti (Beddard & Fedarb, 1895)

Perichaeta everetti Beddard & Fedarb, 1895 : 69 ; Beddard, 1895 : 428 (non *Amynthas stelleri everetti* : Michaelsen, 1899 : 43).

Perichaeta papillata Beddard & Fedarb, 1895 : 71 ; Beddard, 1895 : 428.

Perichaeta sarawacensis Beddard & Fedarb, 1895 : 71 ; Beddard, 1895 : 429.

Perichaeta barami Michaelsen, 1896 : 203.

Amynthas stelleri barami : Michaelsen, 1899 : 41.

Perichaeta stelleri : Michaelsen, 1896 : 202 ; (non Michaelsen, 1891 : 39) ; Horst, 1899 : 205.

Amynthas stelleri (*typica*) : Michaelsen, 1899 : 83.

Pheretima stelleri (*typica*) : Michaelsen, 1922 : 25.
? *Pheretima* (*Pheretima*) *stelleri* (*typica*): Ude, 1932 : 146.
Amynthas stelleri seriatus : Michaelsen, 1899 : 44.
Amynthas stelleri klabatensis Michaelsen, 1899 : 46.
Amynthas stelleri bonensis Michaelsen, 1899 : 45.
Pheretima stelleri bonensis : Michaelsen, 1900 : 307.
[non *Pheretima* (*Pheretima*) *stelleri bonensis* : Michaelsen, 1934a : 108 (= *M. phacellotheca*)]
Pheretima stelleri koroensis Michaelsen, 1910b : 109.
Pheretima stelleri mahakkami Michaelsen, 1922 : 25.
Pheretima (*Pheretima*) *beranensis* Michaelsen, 1928 : 23.
Pheretima (*Pheretima*) *baritoensis* Michaelsen, 1932 : 9.
? *Pheretima* (*Pheretima*) *elongata* : Ude, 1932 : 155 ; (non *Perichaeta elongata* Perrier, 1872).
Pheretima (*Polypheretima*) *beranensis tinjarana* Michaelsen, 1934b : 25.
Metapheretima elongata species-complex [series B (part)] : Sims & Easton, 1972 : 253.

TYPE LOCALITY. Balabac Island, Palawan. Beddard & Fedarb reported that the type locality of *Perichaeta everetti* is Mt Kinabalu, Sabah. The type series of this species in the collections of the British Museum (Natural History) is labelled as originating from Balabac Island, Palawan. Although Beddard & Fedarb wrote in their introduction that the collection they were reporting was collected from both Borneo and Palawan, no reference to Palawan is made in the general text. It is

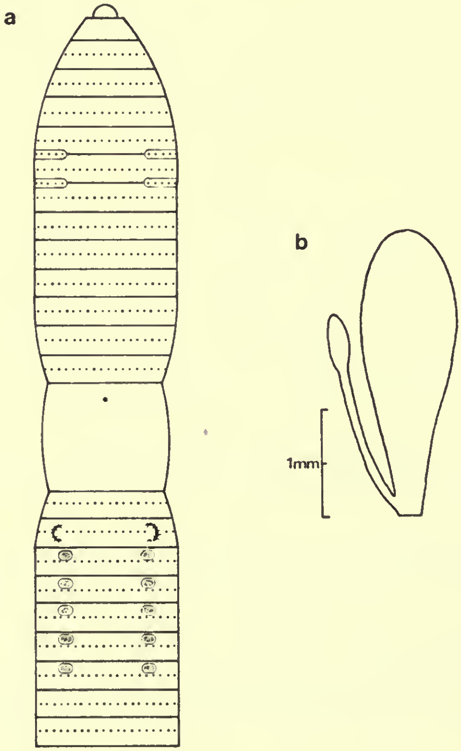

FIG. 5. *Metapheretima everetti*. (a) Diagram of the papillae pattern on the ventral surface of the anterior region of the body. (b) Spermatheca.

proposed to follow Recommendation 72E of the International Code of Zoological Nomenclature and redesignate Balabac Island, Palawan as the type locality for *Perichaeta everetti* Beddard & Fedarb, 1895.

DIAGNOSIS. *M. elongata* species-complex with numerous setae (up to 130 on *vii* in large individuals) and intermediate-sized spermathecal batteries (usually 6–12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. *Indigenous records* (Fig. 6) : north and west Celebes ; Balabac Island, Palawan ; Borneo (up to altitudes of 2400 m) ; Lombok (*c.* 350–450 m only).

This species is unknown outside its indigenous range.

REMARKS. On Lombok this species has been recorded only from localities at altitudes between 350 and 450 m. (Samples from lower altitudes contained the species *elongata* which is rare at the higher altitudes. No samples of earthworms are known from above 450 m on Lombok.) Although altitude would appear to be the primary factor governing the distribution of both *everetti* and *elongata*, it should be noted that, on Lombok, the samples of *everetti* were from natural woodland while those of *elongata* were from cultivated land. All the records of *everetti*, *stelleri* and *phacellotheca* from Celebes are from the northern and western region, an area of forest, while the single record of *elongata* (as yet unconfirmed as an indigenous population) is from the southeast which is an area of savannah. On Mt Kinabalu, Borneo, the species *everetti* occurs at altitudes up to 2400 m, being sympatric from 2100 m with the high altitude species *kinabaluensis*.

Although on Lombok and Mt Kinabalu *everetti* is sympatric with other members of the *elongata* species-complex, there is no indication of hybridization among them.

Metapheretima kinabaluensis (Beddard & Fedarb, 1895)

Perichaeta kinabaluensis Beddard & Fedarb, 1895 : 71 ; Beddard, 1895 : 429.
Metapheretima elongata species-complex [*series A* & *series B* (part)]: Sims & Easton, 1972 : 253.

TYPE LOCALITY. Tamburgare, Mt Kinabalu, Sabah, 2350 m (7700 ft).

DIAGNOSIS. *M. elongata* species-complex with few setae (less than 40 on *vii* in large individuals) and intermediate-sized spermathecal batteries (usually 6–12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. *Indigenous records* (Fig. 6) : Mt Kinabalu, Sabah (2100–2750 m).

This species has not been recorded outside its indigenous range.

REMARKS. This species is known only from high altitudes on Mt Kinabalu where the fauna and flora are of a distinct montane type. It is probable that future investigations of the high-altitude earthworm fauna in the Borneo–Celebes area will reveal other population of this species. Although samples collected at 2100 and 2400 m on Mt Kinabalu contained both *everetti* and *kinabaluensis* there is no indication of hybridization between these two forms.

Metapheretima phacellotheca (Michaelsen, 1899)

Amynthas phakellotheca (sic) Michaelsen, 1899 : 47.
Amynthas phacellotheca : Beddard, 1900 : 640.
Pheretima phacellotheca : Michaelsen, 1900 : 293 ; Gates, 1961 : 304.
Pheretima (*Polypheretima*) *phacellotheca* : Michaelsen, 1934b : 15.
Metapheretima phacellotheca : Sims & Easton, 1972 : 233.
Pheretima (*Pheretima*) *stelleri bonensis* : Michaelsen, 1934a : 108 ; (non *Amynthas stelleri bonensis* Michaelsen, 1899 : 45).

TYPE LOCALITY. Mt Masarang, above Tomohon, northeast Celebes.

DIAGNOSIS. *M. elongata* species-complex with numerous setae (up to 80 on *vii* in large individuals) and large spermathecal batteries (9–12 spermathecae in each battery in large individuals) in furrow 5/6. Spermathecal batteries present in aclitellate as well as clitellate specimens.

DISTRIBUTION. *Indigenous records* (Fig. 6) : northeast Celebes, Buru.
This species has not been recorded outside its indigenous range.

REMARKS. This species is the only member of the *elongata* species-complex known from Buru which is the most easterly indigenous record of the complex. Morphologically it most closely resembles *stelleri* from which it may be distinguished only by the restriction of spermathecal batteries to furrow 5/6. Its relationships with *everetti* and *stelleri*, which also occur in north Celebes, are unknown.

Metapheretima stelleri (Michaelsen, 1891)

Perichaeta stelleri Michaelsen, 1891 : 39 ; (non Michaelsen, 1896 : 202 ; Horst, 1899 : 205).
[non *Amynthas stelleri* (*typica*) : Michaelsen, 1899 : 83.]
[non *Pheretima stelleri* (*typica*) : Michaelsen, 1922 : 25.]
Pheretima (*Pheretima*) *stelleri* (*typica*) : Michaelsen, 1934a : 108 (non Ude, 1932 : 146).
Amynthas stelleri annectens : Michaelsen, 1899 : 42.
Amynthas stelleri everetti : Michaelsen, 1899 : 43 ; (non *Perichaeta everetti* Beddard & Fedarb, 1895 : 69).

TYPE LOCALITY. Sangihe.

DIAGNOSIS. *M. elongata* species-complex with very numerous setae (up to 130 on *vii* in large individuals) and large spermathecal batteries (up to 28 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. *Indigenous records* (Fig. 6) : Kepulaud Taulaud ; Sangihe ; north Celebes.
This species has not been recorded outside its indigenous range.

REMARKS. In Celebes *stelleri* has been recorded from Bone Valley (*c*. 400 m) and the Matinang range (*c*. 1500 m). In both of these areas *everetti* has also been recorded but the relationship between the two species and the factors governing their distribution are unknown. No information is available regarding the relationship between *stelleri* and *phacellotheca*.

DISTRIBUTION

All the records attributed to *everetti*, *stelleri*, *kinabaluensis* and *phacellotheca* (groups 2, 3, 4 and 5) are from Borneo, Celebes or nearby islands and it is considered that these records indicate the indigenous ranges of the species. The species *elongata* (group 1) has been recorded from islands as far apart as Luzon, New Guinea and Sumatra in the Indo-Australasian Archipelago (as well as many other localities throughout the world) but it is thought that this distribution is not entirely natural and that it has been augmented through accidental introduction by man. In the area adjacent to the range of the other members of the complex *elongata* has been recorded from Sumatra, Java, Madura, Bali, Lombok, Sumbawa, Komodo, Gt Bastard Island, Celebes, Kepulaud Taulaud and the Philippines and it is suspected that at least some of these records are from indigenous populations. Among these localities Lombok and Celebes are of particular interest since the most closely related member of the complex, *everetti*, has also been recorded from these islands.

Although the majority of species of the *Pheretima* group possess normal hermaphrodite reproductive systems and are assumed to reproduce only sexually, several species are known to occur as morphs lacking portions of the reproductive system. Gates (1972) recognized four principal morphs: H morph, the normal hermaphrodite form; A morph, lacking spermathecae; R morph, lacking male terminalia; and Z morph, lacking testes. (In addition to these basic forms he also recognized AR and ARZ morphs.) He considered that, with the exception of the H morph, all these forms reproduced by parthenogenesis. He recorded 70 species of the *Pheretima* group from Burma of which 42 were known only from Burma and the adjacent area while 19 were peregrine; only 6% of the indigenous species but 47% of the peregrine forms are known to possess non-hermaphrodite morphs. This correlation between non-hermaphrodite morphs and peregrine distributions led Gates (1956) to suggest that the peregrine species *Metaphire anomala* (Michaelsen, 1907) had originated from eastern Burma where the H morph was more common.

TABLE 3

Population characteristics of *M. elongata* from selected islands

Island	Number of clitellate specimens examined	Proportion of H morphs (%)
Jamaica	84	18
Sumatra	47	15
west & central Java	13	15
east Java	22	50
Madura	3	(2)*
Bali	27	44
Lombok	19	26
Sumbawa	59	51
Komodo	4	
Kepulaud Taulaud	1	(0)*
Philippines	9	(1)*

* For small samples (less than 10 individuals) the number of thecate individuals (rather than the percentage) has been recorded and placed in parentheses.

Metapheretima elongata similarly occurs as H and A morphs so if the hypothesis is valid then the H morph will be more common in its indigenous range than elsewhere. Samples of island populations were examined and the incidence of H morphs was calculated from among the clitellate portion of each series. The results of this study are shown in Table 3. (Java was treated as two regions since it may be considered to be composed of two ecologically distinct areas, tropical rain forest in central and west Java and savannah in east Java.) To obtain a comparative value for a population which was known to be introduced, the incidence of H morphs was assessed in a population from Jamaica. The low incidence of H morphs in the introduced Jamaican population (18%) agrees very well with that of the populations from central and west Java and Sumatra (both 15%) but contrasts strongly with populations from east Java, Bali, Sumbawa and Komodo (44–51%). The value calculated for Lombok (26%) is intermediate between the two classes and somewhat anomalous in view of the geographical position of the island. Possibly the small size of the sample may be the causative factor. Assuming the basic assumption to be valid, these calculations indicate that *elongata* is indigenous in east Java, Bali, Lombok, Sumbawa and Komodo, while the form which is morphologically the most similar, *everetti*, occurs at high altitudes (*c.* 400 m) in Lombok. These values are consistent in the degree of magnitude with those recorded by Gates (1956) when he recorded 20% H morphs of *anomala* in eastern Burma but only 0–7% in other parts of Burma.

Samples from Kepulaud Taulaud, Philippines and Madura were too small to derive any reliable conclusions from them but it seems unlikely that *elongata* is indigenous in either Kepulaud Taulaud or the Philippines, although it may possibly occur naturally in Madura. There have been single inconclusive records of *elongata* from south-east Celebes and Gt Bastard Island but in the former case the specimens cannot be located and in the latter the single extant specimen proved to be indeterminate and the occurrence of indigenous populations of *elongata* in both of these islands has yet to be confirmed. The known indigenous distributions of the members of the *elongata* species-complex are shown in Fig. 6. The earthworm fauna of south-east Asia has been extensively studied (Gates, 1972) and data from this work and other recent collections in the British Museum (Natural History) have allowed the establishment of the western limit of the indigenous range of the complex. Unfortunately the earthworm faunae of the Philippines, Celebes, Moluccas and Lesser Sunda Islands still require considerable study and it is not practical to establish the northern and eastern limits of the distribution of the complex. However, recent extensive collecting in New Guinea (Easton, in preparation) indicates that the complex is absent from this island except for introduced populations of *elongata*.

The form *kinabaluensis* is known only from Mt Kinabalu, Sabah, at altitudes of over 2100 m. It is probable that future collections will reveal that it also occurs on some of the other high mountains in Borneo and possibly even Celebes. Likewise the occurrence of *everetti* in Lombok at altitudes of 400 m may indicate that it occurs at high altitudes throughout the Lesser Sunda Islands.

Metapheretima stelleri has been recorded from Sangihe, Kepulaud Taulaud and north Celebes. Michaelsen (1934b) was of the opinion that this species had been

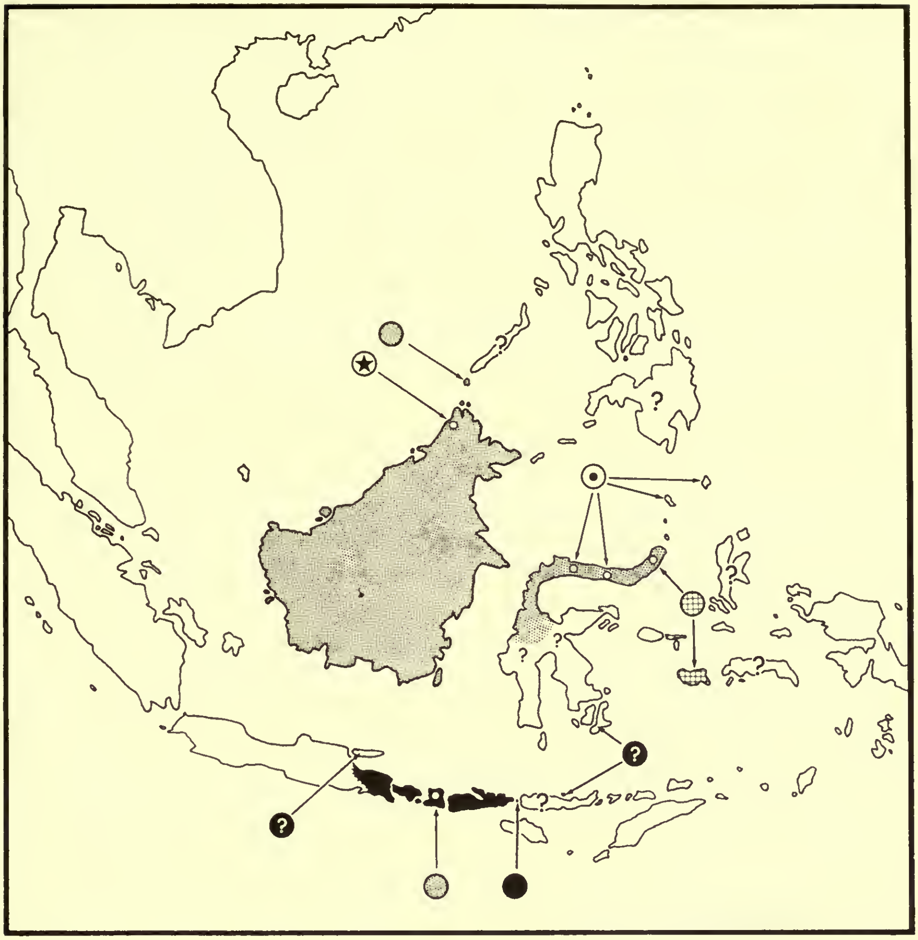

FIG. 6. *Metapheretima elongata* species-complex. Endemic distributions: ● *elongata*; ◍ *everetti*; ✪ *kinabaluensis*; ⊕ *phacellotheca*; ⊙ *stelleri*; ? limits of range uncertain; o isolated or minor localities.

introduced into both Sangihe and Kepulaud Taulaud, but this view is inconsistent with the species' restricted distribution in Celebes. (At the time of Michaelsen's paper the species was thought to be widespread in both Borneo and Celebes.) The wide distribution of the species-complex, crossing both the Flores Sea and the Makassar Strait, suggests that the complex is of considerable antiquity and *M. stelleri* may have reached both Sangihe and Kepulaud Taulaud at a time when land bridges existed between these islands and Celebes.

In Celebes the ranges of each of the three forms occurring there as well as the natural occurrence of *elongata* have still to be established.

ACKNOWLEDGEMENTS

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APPENDIX

MATERIAL EXAMINED AND OTHER RECORDS FROM THE INDO-AUSTRALASIAN ARCHIPELAGO

Museums :

Amsterdam	Zoologisch Museum, Universiteit van Amsterdam
Berlin	Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
BM(NH)	British Museum (Natural History), London
Bogor	Museum Zoologicum Bogoriense, Bogor
Hamburg	Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg
Leiden	Rijksmuseum van Natuurlijke Historie, Leiden
Paris	Museum National d'Histoire Naturelle, Paris

The suffixes C and A refer to the numbers of clitellate and aclitellate individuals in each series respectively.

Metapheretima elongata (Perrier, 1872)

1. MATERIAL COLLECTED BY DR G. A. LINCOLN DURING THE BRITISH UNIVERSITY DRAGON EXPEDITION, May–September 1973. BM(NH) 1975.7.59-302.

Sumatra : Simabur, 1C ; Sungalamas, 4C 5A ; Kalianda, 6C.

Java : village 16 km north of Balaradja, 1C ; plantation 11 km west of Tomo, 11C 5A ; Krijan, 3C ; cultivated area 6 km east of Bangil, 10C 2A ; Pasir Putih, 7C 4A ; Baluran, 1C ; Sukamade, 2C.

Bali : Udjung, 15C 1A ; foothills 8 km north of Klungkung, 12C 12A.

Lombok : Surawadi, 1C ; Songian, 26C 11A

Sumbawa : Alas, 15C ; Kanar, 14C ; Lape, 7C ; Lampang, 9C ; Napa, 9C 1A ; cultivated area 5 km east of Dompu, 10C 11A ; forest 8 km west of Bolo, 7C 1A.

Komodo ; Komodo village, 4C.

2. OTHER MATERIAL EXAMINED.

Philippines : Bataan, Luzon, 4C, Paris AE 634, 638, 643 (*elongata* : Jamieson, in press) ; Mindoro, 6C, Paris AE 639–642, 644* (*elongata* : Jamieson, in press) ; Manila, Luzon, 2C 1A, BM(NH) 1904.10.5.1–2 (*biserialis* : Beddard, 1890 ; syntypes of *acystis*).

Kepulaud Taulaud : Salibaboe Liroeng, Salibaboe Island, 1C 1A, Amsterdam V.ol 254 (*elongata* : Michaelsen, 1934a).

Sumatra : Bindjey Estate, 3C 1A, Hamburg v.352 (*biserialis* : Michaelsen, 1899) ; north-east Sumatra, 2C 1A, Hamburg v.5060 ; Poeloe-Weh, 33C 11A, Leiden 1879, 1882, 1887, 1888 (*elongata* : Michaelsen, 1922) ; Nias Island, 1A, Leiden.

Madura : 3C 1A, Leiden 1880, 1883 (*elongata* : Michaelsen, 1922).

Java : Cimaja, Pelabuhanratu, 15C 1A, Bogor Ann. 090 & BM(NH) 1975.5.1–4.

Flores : Groot Bastaard Island, 1 macerated specimen, Leiden 1886 (*elongata* : Michaelsen, 1922).

Jamaica : 84C, 99A ; BM(NH).

3. OTHER RECORDS FROM THE INDO-AUSTRALASIAN ARCHIPELAGO.

Kei Islands : Elat, Gross Kei (*elongata* : Michaelsen, 1910).

Java : Malang (*elongata* : Michaelsen, 1922).

Celebes : Boeton (*elongata* : Ude, 1932).

New Guinea : Kila Kila, Madang district (*elongata* : Sims & Easton, 1972).

Metapheretima everetti (Beddard & Fedarb, 1895)

1. MATERIAL COLLECTED BY DR G. A. LINCOLN DURING THE BRITISH UNIVERSITY DRAGON EXPEDITION, August 1973. BM(NH) 1975.57–58, 303–313.

Lombok : Bentak, 11C 2A.

2. OTHER MATERIAL EXAMINED.

Celebes : Minahassa, 1C, Hamburg v.3836 (*barami* : Michaelsen, 1896) ; —,† 2C 1A, Hamburg v.5197, 5198 (types of *stelleri seriatus*) ; Klabat, 1C, Hamburg v.5196 (holotype of *stelleri klabatensis*).

---

* A specimen from this series was examined by Sims & Easton (1972 : 254) and referred to as a syntype of *Perichaeta biserialis* Perrier, 1875. Further information has now been obtained and it is now certain that the specimen is not typical since it was not collected until 1876.

† The material on which the subspecies *stelleri seriatus* was described came from the Uangkahulu valley; north side of Matinang range; south side of Matinang range and Buol. There is no indication from which of these localities the two series in the Hamburg Museum were collected.

Palawan : Balabac Island, 2C, BM(NH) 1904.10.5.38–40 (syntypes of *everetti*).

Borneo : Mt Kinabalu, Sabah, 6C 3A, BM(NH) 1971.19.12–20 [*series A* (part), *series B* (part) : Sims & Easton, 1972] ; Baram river, Sarawak, 1C, Hamburg v.3835 (holotype of *barami*) ; Labuan, 1C, BM(NH) 1904.10.5.150 (holotype of *sarawacensis*) ; Sarawak, 8C 6A, BM(NH) 1904.10.5.1336–1340 ; Long Lejok, Sarawak, 6C 13A, BM(NH) 1933.10.6.36–42 & Hamburg v.11956 (*stelleri everetti* : Michaelsen, 1934) ; Tinjar river, Long Lejok, Sarawak, 8C 10A, BM(NH) 1933.10.6.12–20 & Hamburg v.11951 (syntypes of *beranensis tinjarana*) ; Merabah, Sarawak, 14C 12A, BM(NH) 1904.10.5.1265–70 (syntypes of *papillata*) ; Putussibau, Kalimanton, 10C 13A, Leiden 1091 (*stelleri* : Horst, 1899) ; Nangaraun, Kalimanton, 5C 9A, Leiden 1903 (*stelleri* : Horst, 1899) ; 'the Liang Koeboeng' (the exact location of this locality could not be established), 1C, Leiden 1904 (*stelleri* ; Horst, 1899) ; Bendjermasin, Kalimanton, 1C, Hamburg v.4024 [*stelleri* (*typica*) : Michaelsen, 1899] ; Bo river, Kalimanton, 3C, Leiden 1900 & Hamburg v.9307 [*stelleri* (*typica*) : Michaelsen, 1922] ; above Mahakkam rivers, Kalimanton, 1C, Leiden 1897 (holotype of *stelleri mahakkami*) ; Birang river, Beran district, Kalimanton, fragments of one or more specimens, Hamburg v.10576 [type(s) of *beranensis*].

Lombok : Swela, 1C, Berlin 7214 [this specimen is here separated from the type series of *Metapheretima badia* (Ude, 1932)].

3. OTHER RECORDS.

Celebes : Koro valley [type(s) of *stelleri koroensis*] ; Bone valley (types of *stelleri bonensis*).

Borneo : Baram river, Sarawak (*stelleri* : Michaelsen, 1896) ; Dorf Poh Trap, Brunei [*stelleri* (*typica*) : Ude, 1932] ; Boentok, on the Barito river, Kalimanton [type(s) of *baritoensis*].

Metapheretima kinabaluensis (Beddard & Fedarb, 1895)

1. MATERIAL EXAMINED.

Borneo : Mt Kinabalu, Sabah, 12C 2A, BM(NH) 1971.19.1–11, 21–23 [*series A* (part), *series B* (part) : Sims & Easton, 1972].

2. OTHER RECORDS.

Borneo : Tamburungare, Mt Kinabalu, Sabah [type(s) of *kinabaluensis*].

Metapheretima phacellotheca (Michaelsen, 1899)

MATERIAL EXAMINED.

Celebes : Mt Masarang, above Tomohon, several spermathecae and fragments of body wall, Hamburg v.5195 [type(s) of *phacellotheca*].

Buru : between Mnges'wain and Leksula, 1C, Amsterdam V.ol 302 (*stelleri bonensis* : Michaelsen, 1934) ; Leksula, 1C, Amsterdam.

Metapheretima stelleri (Michaelsen, 1891)

1. MATERIAL EXAMINED.

Sangihe : —, 7C 1A, Hamburg v.338, BM(NH) 1904.10.5.162 & Leiden 1903 (syntypes of *stelleri*).

Kepulaud Taulaud : Lobo, Karakelang, 1C, Amsterdam V.ol 303.

2. OTHER RECORDS.

Celebes : Matinang range (*stelleri everetti* : Michaelsen, 1899) ; Bone valley [type(s) of *stelleri annectens*].

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THE TAXONOMY OF *CONCHOECIA* (OSTRACODA, HALOCYPRIDIDAE) OF THE *GAUSSI* AND *EDENTATA* GROUPS FROM THE NORTHEAST ATLANTIC WITH A NOTE ON THEIR ECOLOGY

A. J. GOODAY

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BY
ANDREW JOHN GOODAY
Institute of Oceanographic Sciences

Pp 55–100 ; 22 *Text-figures*

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THE TAXONOMY OF *CONCHOECIA* (OSTRACODA, HALOCYPRIDIDAE) OF THE *GAUSSI* AND *EDENTATA* GROUPS FROM THE NORTHEAST ATLANTIC WITH A NOTE ON THEIR ECOLOGY

By A. J. GOODAY

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SYNOPSIS

Conchoecia subedentata sp. n. and *C.* aff. *edentata* are described from the Northeast Atlantic and placed in a new *edentata* species group based on *C. edentata*, an Antarctic species. *C. edentata* was previously assigned to the *gaussi* group which is here restricted to *C. gaussi* and *C. incisa*, both of which are redescribed.

C. subedentata sp. n. and *C.* aff. *edentata* are commonest at 60°N and decrease in abundance southwards. *C. subedentata* sp. n. occurs mainly between 300 m and 900 m depth, *C.* aff. *edentata* is most frequent below 800 m. *C. gaussi* is most abundant at 53°N and *C. incisa* at 30°N. *C. incisa* males are rare and restricted to below 1250 m, while females and juveniles have two peaks of abundance, below 800 m and between 600 m and the surface. *C. gaussi* occurs mainly below 1000 m. None of the species appears to undergo diurnal vertical migration except for females and juveniles of *C. incisa* where all specimens in the top 200 m were taken at night.

Taken together adults and juveniles of *C. gaussi* and *C. incisa* fall into three or four size classes which may have some trophic significance.

INTRODUCTION

Skogsberg (1920 : 676) proposed the *gaussi* group of species to include *Conchoecia incisa* Müller, 1906 and *Conchoecia gaussi* Müller, 1908. Later Rudyakov (1962) placed *C. edentata* Müller, 1906 close to *C. gaussi* and Deevey (1974 : 368) included it

TABLE 1

Station details and gear used

STATION	LOCATION IN NORTHEAST ATLANTIC	DATE	*Discovery* CRUISE NO.	GEAR
5814	28°N, 14°W	Sept. to Dec. 1965	8	N113
5816				
5818				
5819				
5823				
5825				
6155	28°N, 14°W	Oct. to Nov. 1966	15	N113
6156				
6164				
6176				
6183	34°N, 80°W			
6193				
6674	11°35′N, 21°26′W	Jan. to April 1968	21	N113 B
7089	18°N, 25°W	Oct. to Dec. 1969	30	RMT 1+8 and N113
7406	48°N, 20°W	Sept. to Nov. 1970	36	RMT 1+8
7478				
7480				
7709	60°N, 20°W	April to June 1971	39	RMT 1+8
7711	53°N, 20°W			
7803	18°N, 25°W	Feb. to April 1972	45	RMT 1+8
7856				
8262	32°N, 16°W	Feb. to March 1973	52	RMT 1+8
8264	32°N, 24°W			
8265	32°N, 27°W			
8270	34°N, 34°W			
8271	34°N, 39°W			
8272	34°N, 43°W			

in the *gaussi* group, while in a revision of *Conchoecia* Poulsen (1973 : 103) established the genus *Gaussicia* for these three species. Unfortunately some of the genera into which Poulsen subdivided *Conchoecia* are questionable. In this paper I therefore disregard *Gaussicia* until Poulsen's taxonomy can be thoroughly assessed. I also believe it is wrong to combine *C. edentata* with *C. gaussi* and *C. incisa*. In my view *C. edentata* and its allies described in this paper differ sufficiently from *C. gaussi* and *C. incisa* to warrant their placement in a new *edentata* group.

Plankton samples collected during recent years in the Northeast Atlantic by the RRS *Discovery* have yielded abundant material of the *gaussi* and *edentata* groups. Specimens resembling *C. edentata* predominate and fall into two size classes The larger form is closer to Müller's (1906) original description of *C. edentata* and is assigned here to *C.* aff. *edentata* while the smaller form is described as *C. subedentata* sp. n. In addition, the two poorly known species of the *gaussi* group, *C. gaussi* and *C. incisa*, are redescribed, and the ecology of members of the *gaussi* and *edentata* groups is discussed.

Material and methods

The material was obtained from 27 stations in the Northeast Atlantic during seven cruises by RRS *Discovery* between 1965 and 1973. Details of the stations are summarized in Table 1. On earlier cruises, a 1 m^2 net (N113) fitted with a catch dividing bucket was employed (Foxton, 1969). This was superseded in 1969 by the combination net (RMT 1+8) described by Baker, Clarke & Harris (1973). Most of the ostracods were caught in the RMT 1 part of the combination net although a few adult specimens of *C. incisa* and *C. gaussi* were picked out from the RMT 8 samples.

A few characters measured must be briefly defined here. Carapace length includes the rostrum; carapace height and breadth are maximum values. Segments 1 and 2 of the first antenna are measured along their dorsal margins and the first segment is taken to begin at the base of the frontal organ. Protopodite length includes the anterior hook and segments 2-8 of the second antenna exopodite are measured from the distal end of segment 1 and not from the proximal end of segment 2.

TAXONOMIC SECTION

edentata group

Diagnosis. Both valves bear median ventral glands; asymmetric glands are in usual positions. Male first antenna with long *a* and *c* setae and pad on *b* seta; *e* seta has proximally pointing spines which are difficult to distinguish. Female first antenna has very short dorsal seta, *a–d* setae are slightly longer or just shorter than *e* seta which bears group of proximally pointing spines on distal flattened and widened part. Male second antenna with *g* seta slightly widened and flattened distally; in female, *g* seta is rather wider and sword-shaped. Serrated teeth of mandibular basale low with weak primary cusps. Maxilla with only four posterior setae. Labrum has weak hyaline plate and small weak teeth. Female sixth limb with characteristically long and flexible ventral seta and very short dorsal seta on final segment.

Remarks. *Conchoecia edentata* of Müller (1906) was included with *C. gaussi* and *C. incisa* in the new genus *Gaussicia* (=*gaussi* group) by Poulsen (1973). However this species, together with *C.* aff. *edentata* and *C. subedentata* sp. n. described here, differs from *C. gaussi* and *C. incisa* in numerous characters which are summarized in Table 5. In contrast the points of similarity are rather few: the presence of the ventral gland, the general character of the *b*, *d* and *e* seta armature on the male first antenna, the shape of the female *g* seta (second antenna) and *e* seta (first antenna), the development of minute spines on various segments of the female first antenna and the male and female second antenna and perhaps the same general structure of the cutting edge and tooth lists of the mandibular coxale.

Because of the large number of differences (Table 5) it seems sensible to remove *C. edentata*, *C.* aff. *edentata* and *C. subedentata* sp. n. from the *gaussi* group and place them in a new *edentata* group. The arrangement is supported by the fact that many differences between the two groups are concerned with characters of the mandible, maxilla, fifth and sixth limbs and labrum. These limbs are more conservative in their structure than the first and second antennae and so their characteristics must carry more taxonomic weight.

The *edentata* group is characterized by several features. (i) The development of a median ventral gland; this is also present in *C. gaussi* and in *C. prosadena* the right asymmetric gland (not homologous with the ventral gland in the *edentata* and *gaussi* groups) is situated at the posterior end of the ventral margin. (ii) The *a–d* setae of the female first antenna are slightly shorter or slightly longer than the *e* seta. In no other species of *Conchoecia* do these setae approach the length of the *e* seta. The group of proximally pointing spines with expanded bases on the distal part of the *e* seta are probably also peculiar to this group. (iii) On the terminal segment of the female sixth limb the ventral *a* seta is very long, thin and flexible, the claw-like median *b* seta rather longer or shorter and the dorsal *c* seta is very short. These setae are probably diagnostic for the *edentata* group although characters of the sixth limb have generally been ignored in species descriptions. However, in all species of *Conchoecia* for which information is available the terminal setae of this limb are claw-like and shorter than the two ventral setae of the *edentata* group.

The *edentata* group is probably closely related to the *gaussi* group. It also shares a number of characters with the *mollis* group: distally widened *g* setae on the male and female second antennae and a distally widened *e* seta on the female first antenna, long *a* and *c* setae of the male first antenna and a pad on the *b* seta of this limb. *C. congolensis* Poulsen, 1969, which Poulsen (1969a: 116) felt was related to the *bispinosa* and *gaussi* groups, may be closer to the *edentata* group. In the only known specimen, a female, the dorsal seta is short and the *a–d* setae are long, although not as long as in the *edentata* species group. However the long, rod-shaped capitulum and the absence of a ventral gland distinguish *C. congolensis* from species of both the *edentata* and *gaussi* groups.

Conchoecia subedentata sp. n.

(Figs 2–5)

DIAGNOSIS. Species of *edentata* group characterized by small size (male carapace length 1·123–1·280 mm, mean 1·212 ± 0·030 mm) and setation of final segment of female limb where ventral *a* seta is longer than middle claw *b* seta.

MATERIAL. 1447 specimens comprising 388 females, 392 males and 667 juveniles.

HOLOTYPE AND PARATYPE. The holotype, a male stained with lignin pink and mounted on slides in Euparal, is deposited in the British Museum (Natural History), reg. no. 1974.736. The type locality is *Discovery* station 7711, haul 23; 52°57·1′–52°53·1′N, 20°0·0′–20°3·4′W. Depth 200–300 m. Time 2342–0142 hr. Date 19–20 May 1971. Gear RMT 1+8. The paratype material comprises a dissected female reg. no. 1974.737 and some undissected male and female specimens in 70% alcohol, reg. nos 1974.738–748.

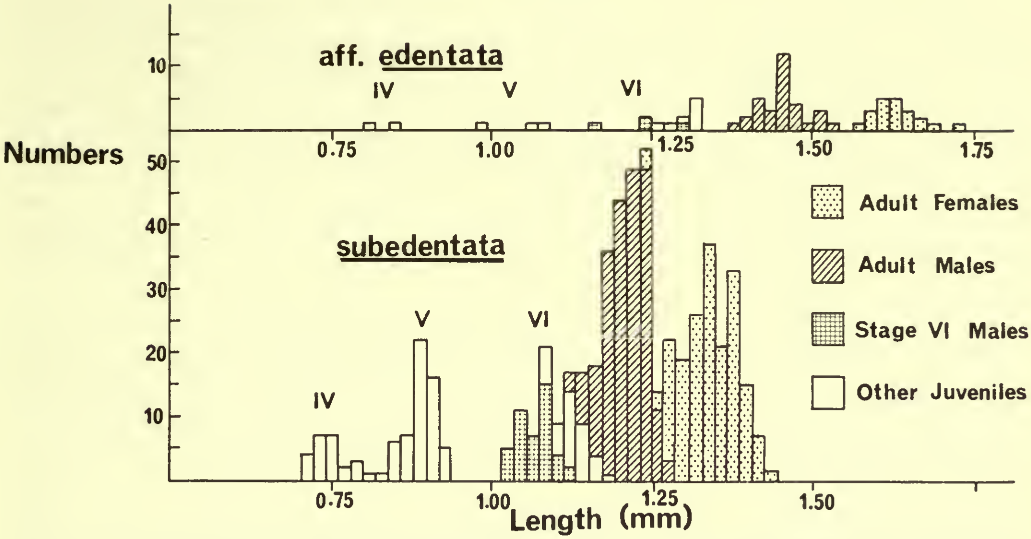

FIG. 1. Histograms showing adult and juvenile carapace lengths of *Conchoecia* aff. *edentata* and *Conchoecia subedentata* sp. n.

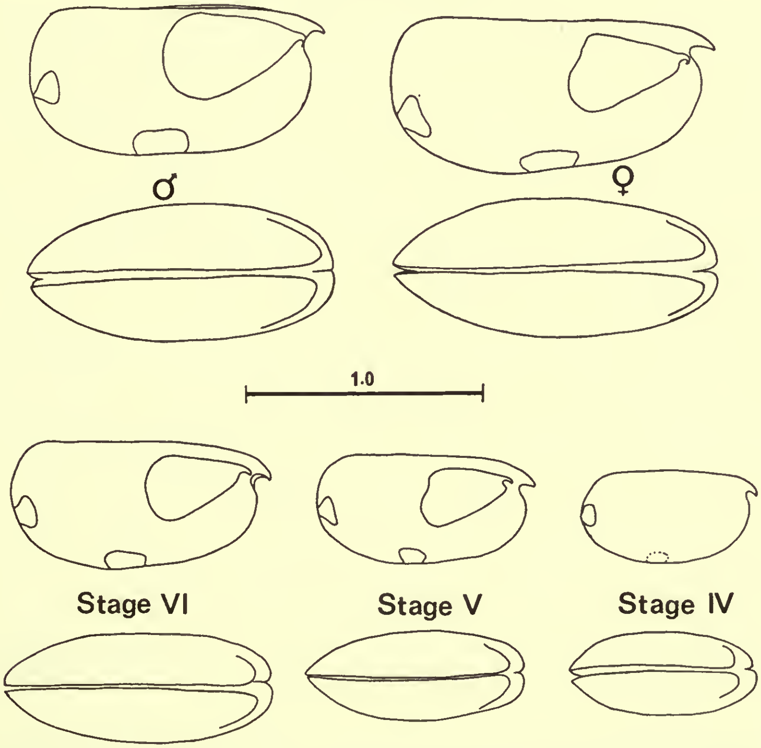

FIG. 2. *Conchoecia subedentata* sp. n. Lateral and ventral carapace outlines of adults and final three juvenile instars.

Description of male. Carapace (Fig. 2). The carapace lengths of 216 specimens range from 1·123 mm to 1·280 mm with a mean value of 1·212 ± 0·030 (Fig. 1). Height is less than half the length, and breadth is about 80% of the height. In lateral view the posterior margin is gently curved, joining the dorsal margin at a rounded angle and the ventral margin evenly. The ventral margin is either straight or slightly curved and the lateral outline narrows slightly towards the anterior end. There is no surface ornamentation. The right asymmetric gland is displaced up the dorsal margin, opening at about $\frac{2}{5}$ of the carapace height. The median ventral gland is as large or rather larger than the right asymmetric gland.

Frontal organ (Figs 3A, C). The stalk extends just beyond the end of the first antenna. The proximal half of the capitulum tapers forwards, while distally the dorsal margin is nearly straight, the ventral margin slightly convex and the end asymmetrically rounded. Proximally, the lower surface of the capitulum bears numerous prominent forward directed spines and the distal part has a few scattered spines.

First antenna (Figs 3A, B). Segments 1–4 are usually bare but occasionally have a few scattered spines. The first segment is shorter than the second. The *a* seta is longer than the limb and swollen near the base; it loops down proximally and then lies parallel to the limb for the rest of its length. The *b* seta is slightly shorter than the *d* seta and bears a distal pad; adjacent to the pad on the anterior side of the seta are 8–11 closely spaced spines preceded proximally by 6–10 widely spaced spines. The *c* seta is somewhat shorter than the *a* seta and usually lies parallel to the antenna. The *d* seta carries 3–5 small anterior spines at a point level with the *b* seta pad, and sometimes has 2–3 posterior spines. The *e* seta armature is difficult to discern. In side view the posterior margin of the seta is raised into 17–22 low 'bumps', in front view the 'bumps' appear as vague paired patches from which arise indistinct and proximally directed spines. This main armature is preceded by 4–7 small anterior spines.

Second antenna (Figs 3D–G). The protopodite surface is bare but the first exopodite segment has numerous minute spines concentrated proximally where they form a dense covering visible only at high magnification. On the first endopodite segment, the processus mammillaris has a rounded end and no terminal tubercule. The *b* seta is about $\frac{3}{4}$ the length of the *a* seta and the long slender upward curving *c* seta is some three times as long as the downward curving *d* seta; the *e* seta is a small spine. The *a*, *b* and *c* setae bear fine hairs. The *f* seta is over $\frac{1}{2}$ the length of the *g* seta; it is thin walled for much of its length and carries 4–7 minute anterior spines. The *g* seta is flattened and slightly widened distally. On the proximal tubular part it has 7–9 anterior and 8–10 posterior spines. The *h*, *i* and *j* setae are shorter than the *f* seta; the *j* seta is rather swollen at its base and bears prominent spines, most on the swollen part but some below. The left hook appendage has a short proximal section, a rounded angle of about 90°, a long slightly curved distal section and a rounded tip with a few indistinct subterminal ridges. The right hook appendage is larger with an angle of about 135° between the proximal and distal sections and about 8 prominent subterminal ridges.

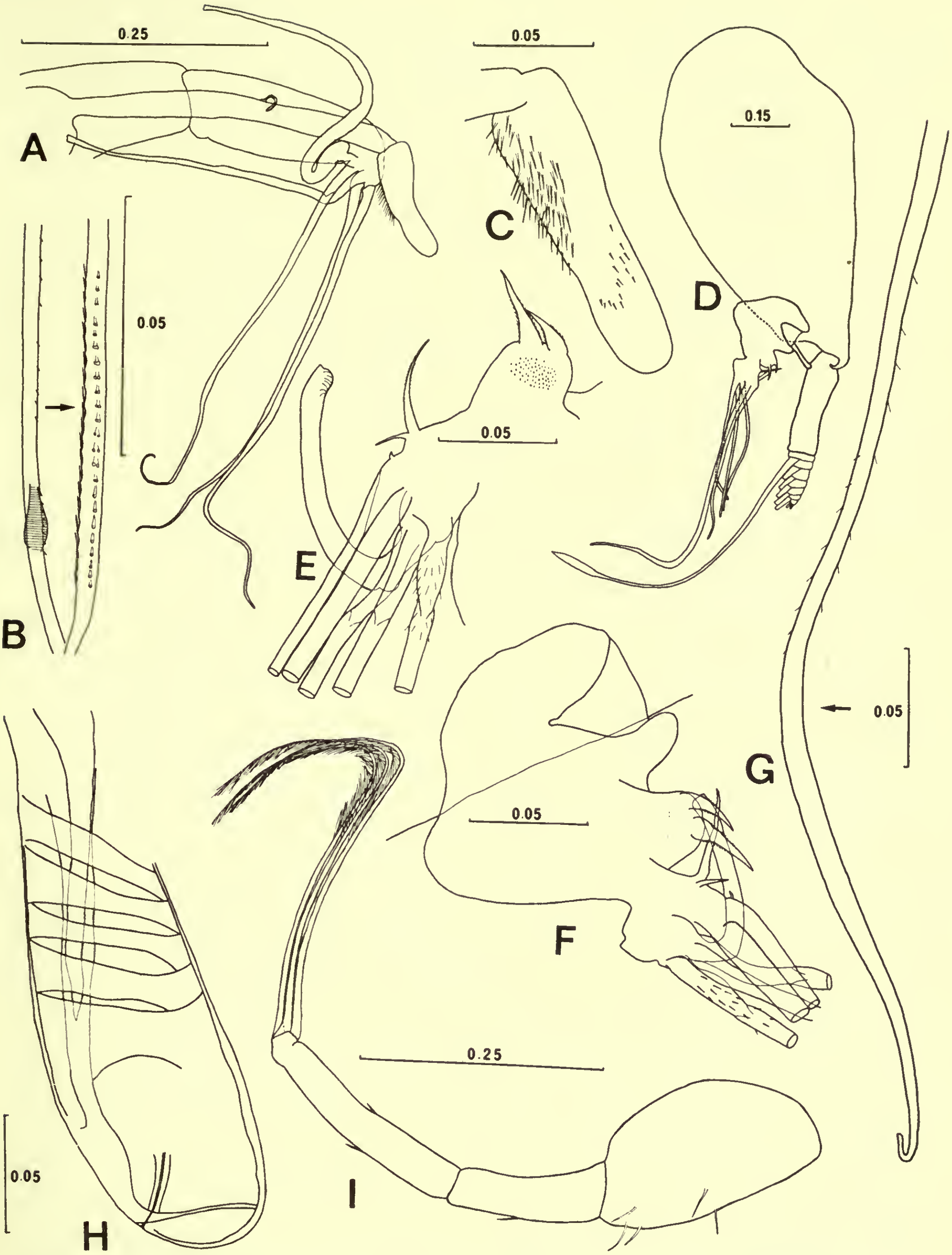
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FIG. 3. Male dimorphic parts of *Conchoecia subedentata* sp. n.; arrow indicates anterior. (A) First antenna and frontal organ. (B) Main armature of *b* and *e* setae of first antenna. (C) Capitulum of frontal organ. (D) Second antenna. (E) Second and third segments of endopodite of right second antenna. (F) Endopodite of left second antenna. (G) *g* seta of second antenna. (H) Penis. (I) Sixth limb.

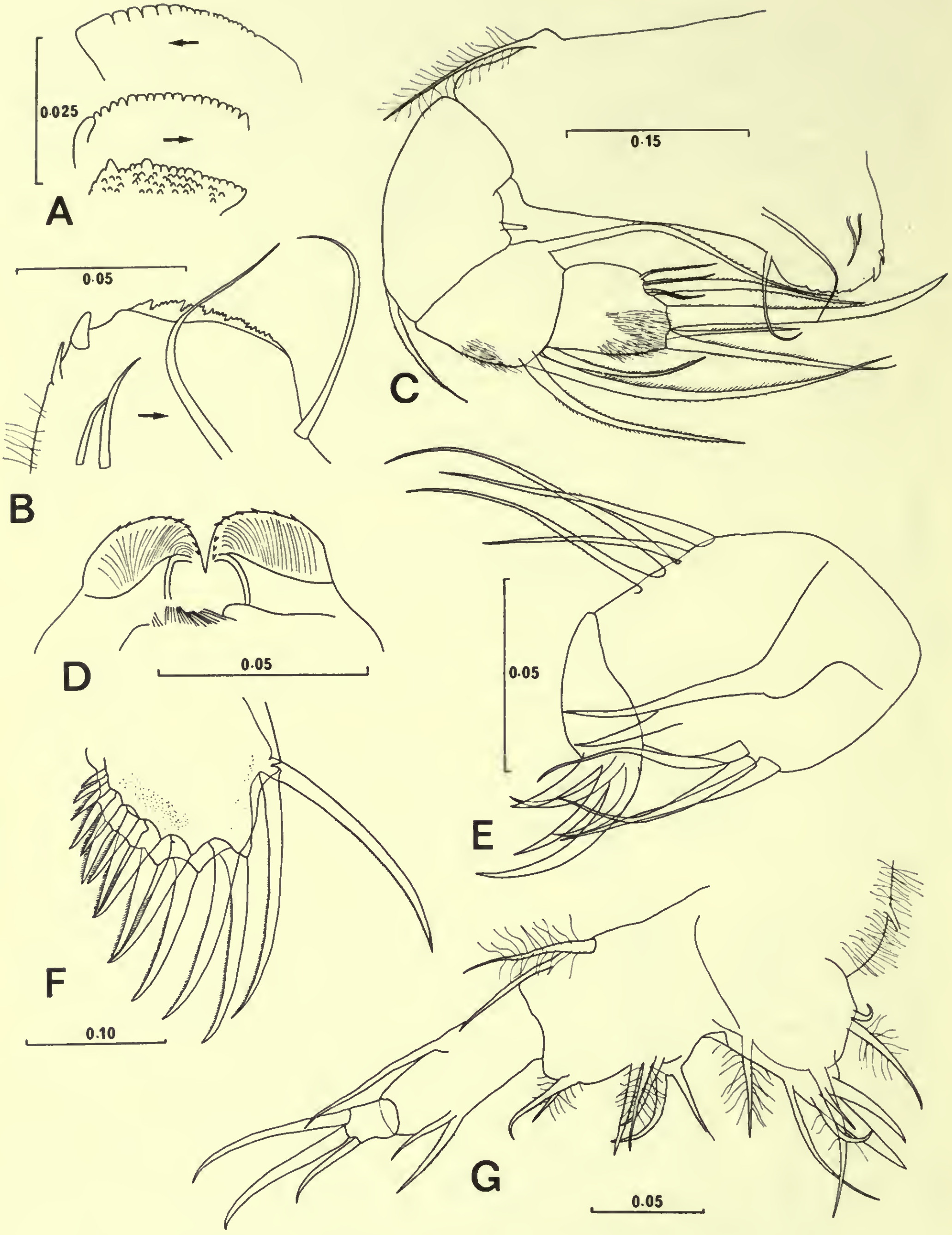


FIG. 4. Non-dimorphic parts of *Conchoecia subedentata* sp. n.; arrow indicates anterior. (A) From top to bottom, cutting edge, distal and proximal tooth lists of mandibular coxale. (B) Cutting edge and adjacent setae of mandibular basale. (C) Basale, endopodite and exopodite of mandible. (D) Labrum. (E) Maxilla. (F) Caudal furca. (G) Fifth limb.

Mandible (Figs 4A–C). The toothed edge of the coxale slopes down posteriorly. It has 19–23 teeth comprising one elongate anterior tooth, 5–6 fairly large teeth and 13–17 small teeth which decrease in size posteriorly; the posterior $\frac{1}{4}$ of the toothed edge lacks teeth. The distal list has a large posterior tooth and 16–19 regular teeth of equal size. The proximal list has a large posterior tooth and 15–19 smaller teeth of rather variable sizes; the inner surface of this list is covered with papillae. The toothed edge of the basale has the usual arrangement of two spine teeth, six serrate teeth and an unusually long and low outer tooth. Only the posterior two serrate teeth have well-defined main cusps; on the remaining teeth, the main cusps are only slightly larger or are indistinguishable from the secondary cusps. There are two short setae near the spine teeth on the inner surface of the basale. The second exopodite segment has some fine hairs on the outer distal edge, the third segment has a more extensive distal area of hairs.

Maxilla (Fig. 4E). The anterior margin has four long setae, the distal two longer than the proximal two. The posterior margin has three setae. The basal seta extends to the end of the limb.

Fifth limb (Fig. 4G). On the dorsal side of the first exopodite segment, the distal seta extends only as far as the base of the dorsal seta on the next segment.

Sixth limb (Fig. 3I). This is typical for the genus.

Labrum (Fig. 4D). The hyaline membrane is fragile with a deep V-shaped notch. On each side of the notch are about nine small inward facing teeth which become more closely spaced towards the inside.

Caudal furca (Fig. 4F). The caudal lamellae are covered with fine hairs.

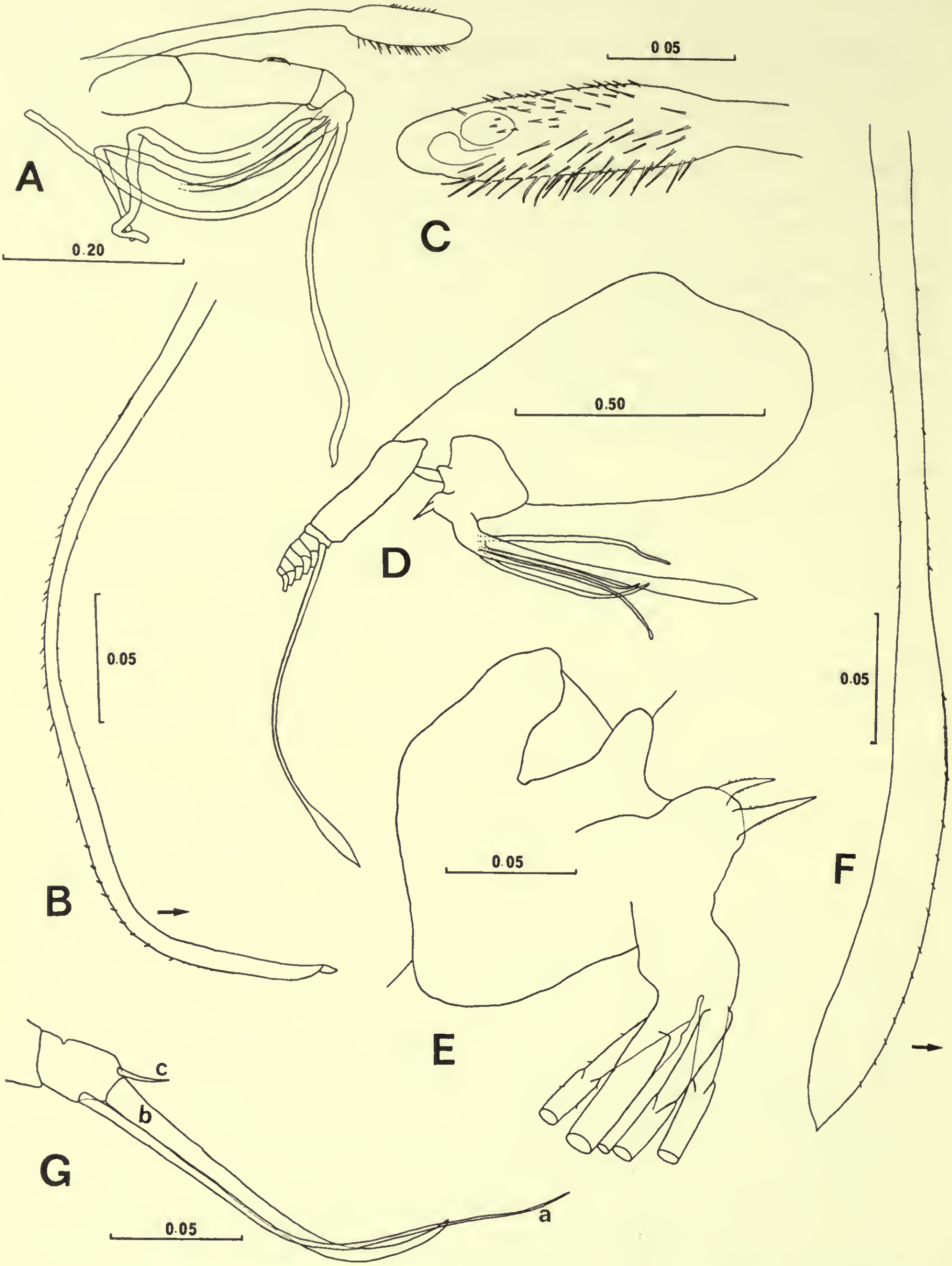
Penis (Fig. 3H). The upper margin is almost straight and the lower margin curved. There are five transverse muscle bands.

DESCRIPTION OF FEMALE. Carapace (Fig. 2). The carapace lengths of 190 specimens range from 1·261 mm to 1·438 mm with a mean value of 1·345 ± 0·041 mm (Fig. 1). Apart from being rather more elongate, the lateral outline is identical to that of the male. There is no surface ornamentation.

Frontal organ (Fig. 5C). The capitulum is distinct from the shaft. It tapers slightly anteriorly, with a rounded end and sometimes a slight concavity below the end. The capitulum is armed with long prominent spines on the ventral half and smaller, rather less, extensive spines dorsally.

First antenna (Figs 5A, B). The second segment is longer than the first and one or both may have a few scattered spines, visible only at high magnification. The dorsal seta is very short; the *a–d* setae are longer than the limb and the *a* seta is somewhat expanded proximally. The *e* seta is rather shorter than the more proximal setae. On the posterior side it bears 29–30 spines of varying sizes. The proximal tubular part of the seta has 16–19 spines of which the first 6–8 are small and difficult to distinguish and the remainder long and prominent. The distal flattened part of the seta bears 3–5 long distally pointing spines followed by 8–12 proximally pointing spines with unusually wide bases and 3–4 minute distally directed spines. On the anterior side are 10–13 spines, about $\frac{1}{2}$ on the distal flattened part of the seta.

Second antenna (Figs 5D–F). The armature of the second exopodite segment and the *a* and *b* setae are as for the male limb. The *f* seta is over $\frac{1}{2}$ the length of the


A
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0 05
C
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D
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F
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E
c
b
G
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a

Fig. 5. Female dimorphic parts of *Conchoecia subedentata* sp. n. ; arrow indicates anterior. (A) First antenna and frontal organ. (B) *e* seta of first antenna. (C) Capitulum of frontal organ. (D) Second antenna. (E) Endopodite of left second antenna. (F) *g* seta of second antenna. (G) Terminal segment and setae of sixth limb.

g seta and in some specimens has 1–2 minute anterior spines. The *g* seta is flattened and widened in its distal half. Posteriorly it bears 19–26 spines of which the proximal 5–8 lie on the tubular part of the seta and on the anterior side it carries 6–8 similar spines, all on the tubular section. The *h, i* and *j* setae are slightly shorter than the *f* seta and the *j* seta bears a few spines proximally.

Sixth limb (Fig. 5G). On the final segment the three setae are here designated *a, b* and *c* from ventral to dorsal (Fig. 5G) and their relative lengths are summarized in Table 4. The *a* seta is thin, long and flexible, the *b* seta is claw-like and shorter than the *a* seta while the *c* seta is a short spine.

JUVENILES (Fig. 2). The range of carapace lengths in 24 Stage IV juveniles is 0·709–0·808 mm (mean 0·745 ± 0·014 mm); 57 Stage V juveniles have a length range of 0·827–0·926 mm (mean 0·888 ± 0·021 mm). Male and female Stage VI instars may be distinguished by the presence of immature eggs in the females and a rudimentary penis and testes in the male. The males are rather smaller (1·024–1·123 mm; mean 1·066 ± 0·013 mm in 44 specimens) than the females (1·084–1·182 mm; mean 1·124 ± 0·019 mm in 37 specimens). Juvenile and adult carapace lengths are summarized in a histogram (Fig. 1).

TABLE 2

Meristic characters of the males of the four described species

	C. subedentata sp. n.		*C.* aff. *edentata*		*C. incisa*		*C. gaussi*
N	216		40		8		10
Length: range (mm)	1·123–1·280		1·400–1·517		1·822–1·911		2·955–3·330
Length: mean, s.d. (mm)	1·210	0·030	1·460	0·027	1·877	0·030	3·138 0·107
N	20		10		8		6
	x̄	s.d.	x̄	s.d.	x̄	s.d.	x̄
Height	46·27	0·90	47·47	1·26	43·66	0·76	44·64
Breadth	40·83	1·24	40·39	1·02	38·49	1·42	40·93
FO shaft	32·30	1·29	31·53	0·69	28·10	0·44	30·33
capitulum	11·51	0·36	11·57	0·69	18·63	1·17	16·52
1st Antenna segment 1	10·07	0·31	11·49	0·70	11·15	0·27	10·99
segment 2	18·09	0·45	16·38	0·43	10·79	0·16	13·93
total	28·84	0·78	27·87	0·62	21·95	0·38	24·92
a seta	36·87	1·49	35·89	1·75	38·44	1·15	22·68
b seta	42·26	0·92	40·40	1·33	46·27	0·84	48·79
c seta	30·63	1·46	30·96	1·92	12·68	0·73	13·21
d seta	42·44	1·03	41·39	1·09	39·86	0·95	49·18
e seta	50·91	1·34	51·81	1·39	51·80	2·25	52·00
2nd Antenna protopodite	53·04	1·32	52·09	0·51	47·72	1·23	46·82
exopodite segment 1	16·80	0·39	17·55	0·27	17·54	0·36	19·26
segments 2–8	8·19	0·31	8·32	0·22	7·95	0·27	7·19
LSS	48·28	1·56	47·70	1·39	48·96	0·28	42·54
g seta	45·96	1·07	48·96	0·48	52·86	1·29	42·77
f seta	24·70	0·94	28·13	1·78	39·46	2·16	39·98
h–j setae	21·44	1·78	22·59	1·29	20·57	1·66	27·31

All measurements, other than the carapace length, are expressed as percentages of the carapace length. The measurements are mean values and are followed by standard deviations. N is the number of specimens measured. LSS is the longest swimming seta. FO is the frontal organ.

REMARKS. *C. subedentata* sp. n. is identical in many respects to *C.* aff. *edentata*. It is compared and contrasted with this form in detail below but the main points may be summarized here. (i) The mean carapace length in *C. subedentata* sp. n. is 81% (♀) to 83% (♂) that of *C.* aff. *edentata* ; (ii) the *f* and *g* setae of the male and female second antennae are proportionally shorter in *C. subedentata* sp. n. (Tables 2

TABLE 3

Meristic characters of the females of the four described species

	C. subedentata sp. n.		*C.* aff. *edentata*		*C. incisa*		*C. gaussi*
N	190		31		39		4
Length: range (mm)	1·261–1·438		1·576–1·734		2·462–2·837		3·369–3·546
Length: mean, s.d. (mm)	1·345	0·041	1·651	0·067	2·624	0·062	3·462
N	20		10		8		4
	x̄	s.d.	x̄	s.d.	x̄	s.d.	x̄
Height	46·08	0·99	47·20	1·29	49·54	1·23	46·94
Breadth	38·37	0·85	38·77	1·12	41·65	1·49	41·08
FO total length	29·83	0·69	28·77	0·74	28·92	0·91	35·58
1st Antenna segment 1	6·75	0·36	6·89	0·52	4·88	0·18	5·73
segment 2	10·33	0·69	9·54	0·70	6·71	0·14	8·25
total	16·98	0·58	16·66	0·65	11·58	0·26	13·13
a–d setae	29·51	1·57	29·15	1·78	11·78	0·84	14·77
e seta	28·77	0·77	33·87	0·02	32·22	0·64	37·02
2nd Antenna protopodite	47·32	0·80	44·96	0·70	38·83	0·83	42·21
exopodite segment 1	15·04	0·72	15·67	0·34	14·23	0·24	17·47
segments 2–8	7·23	0·29	7·25	0·19	6·46	0·17	6·98
LSS	41·42	1·28	42·18	0·84	34·58	1·50	36·47
g seta	32·24	0·34	34·79	0·66	28·14	0·49	33·98
f seta	18·18	0·81	20·27	0·67	19·64	0·91	26·34
h–j setae	22·36	1·05	24·52	1·40	18·49	0·66	28·01

All measurements, other than the carapace length, are expressed as percentages of the carapace length. The measurements are mean values and are followed by standard deviations. N is the number of specimens measured. LSS is the longest swimming seta. FO is the frontal organ.

TABLE 4

Meristic characters of the sixth limb in males and females of *C. subedentata* sp. n. and *C* aff. *edentata*

	C. subedentata sp. n.		*C.* aff. *edentata*	
	♀	♂	♀	♂
N	9	6	6	6
Segment 1	14·32	12·58	14·02	11·97
Segment 2	19·09	17·96	18·71	18·01
Total	33·48	30·55	32·73	29·98
a seta	11·09	37·69	12·59	40·50
b seta	16·51		12·56	
c seta	1·55		3·06	

All measurements are mean values and are expressed as percentages of the carapace length. N is the number of specimens measured.

and 3) and the female *g* seta is relatively wider distally ; (iii) the right hook appendage extends to just above the base of the *c* seta in *C. subedentata* sp. n. but well above this point in *C.* aff. *edentata* ; (iv) on the inner side of the mandibular basale there are two setae near the spine teeth but only one in *C.* aff. *edentata* ; (v) the thin ventral *a* seta of the female sixth limb extends well beyond the end of the middle claw *b* seta in *C. subedentata* but not to the end of the *b* seta in *C.* aff. *edentata* and the short dorsal *c* seta in *C. subedentata* sp. n. is about twice the proportional length of this seta in *C.* aff. *edentata* (Table 4).

The characters which separate *C. subedentata* sp. n. and *C.* aff. *edentata* also distinguish *C. subedentata* sp. n. from previously described and figured specimens of *C. edentata.* Thus *C. subedentata* sp. n. is much smaller than *C. edentata* and differs from the figured male of Müller (1906 : pl. XV, fig. 2a) and Rudyakov (1962 : fig. 12), in having a shorter right hook appendage and from the females of Barney (1921 : fig. 5F) and Rudyakov (1962 : fig. 11E) in the relative lengths of the terminal setae on the sixth limb and from Rudyakov's (1962 : fig. 13B) figured specimens in the presence of two setae rather than one next to the spine teeth on the mandibular basale.

Geographical distribution. In the Northeast Atlantic this previously unrecorded species was found at the following stations ; the number of specimens caught at each station is given in parentheses : Station 7709, 60°N, 20°W (708) ; Station 7711, 53°N, 20°W (408) ; Stations 7406 (245), 7478 (14) and 7480 (1) all 40°N, 20°W ; Stations 8262 (1), 8264 (2), 8265 (1), 8270 (4), 8271 (4), 8272 (3), all along 32°N, ; Station 7856, 30°N, 23°W (63), Station 7089, 18°N, 25°W (3). The depth distribution at different latitudes is summarized in Fig. 19.

Conchoecia aff. **edentata** Müller 1906

(Figs 6–9)

Material. Ninety-nine specimens comprising 26 females, 43 males and 30 juveniles. Dissected male and female specimens, stained with lignin pink and mounted in Euparal, are deposited in the British Museum (Natural History), reg. nos 1974.749 and 750.

Description of male. Carapace (Fig. 6). The carapace lengths of 40 specimens range from 1·399 mm to 1·517 mm with a mean value of 1·459 ± 0·027 mm (Fig. 1). The lateral outline and gland positions are as for *C. subedentata* sp. n. There is no surface ornamentation.

Frontal organ (Fig. 7D). As for *C. subedentata* sp. n.

First antenna (Figs 7A, C). Segments 1 and 2 are together proportionally rather longer than in *C. subedentata* sp. n., are usually bare but may have a few scattered spines. The *a–e* setae have about the same proportional lengths as in *C. subedentata* sp. n. and similar armature. The *b* seta bears 9–12 widely spaced spines and 8–10 more closely spaced and rather weaker spines level with the pad. The *d* seta carries 6–12 weaker anterior spines and sometimes a few similar posterior spines while the *e* seta has 19–25 paired 'bumps' from which arise indistinct spines.

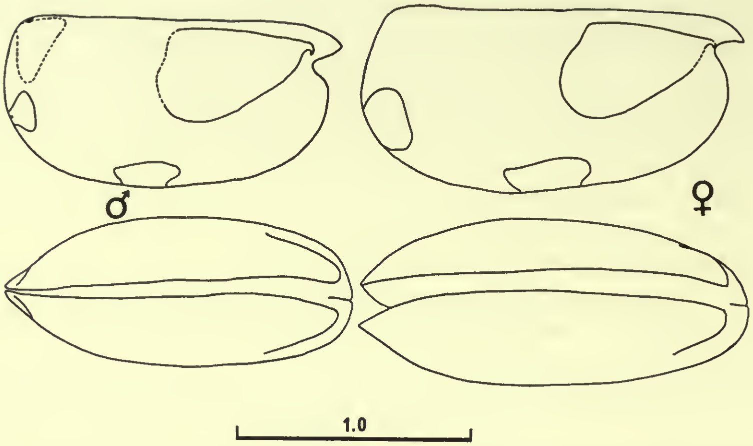


FIG. 6. *Conchoecia* aff. *edentata*. Lateral and ventral carapace outlines of adults.

Second antenna (Figs 7B, E–G). The proportional lengths and armature of the limb segments are as for *C. subedentata* sp. n. but the *f* and *g* setae are proportionally longer (Table 2). The *f* seta bears 5–7 minute anterior spines. The *g* seta has 6–11 small proximal and median posterior spines and 6–9 similar, mainly median spines on the anterior surface ; the distal flattened part of this seta is bare. The remaining setae are as described for *C. subedentata* sp. n. Also the right hook appendage is markedly longer in *C.* aff. *edentata*, extending well above the bases of the *c* and *d* setae, but only just above this point in *C. subedentata* sp. n.

Mandible (Figs 8A–C). The toothed edge, the proximal and distal lists of the coxale and the basale toothed edge have the same structure as in *C. subedentata* sp.n. The toothed edge of the coxale bears 15–19 teeth comprising a broad posterior tooth, five large teeth and 10–13 small teeth. The distal list has a large curved posterior tooth and 18–21 smaller teeth of equal size, while the proximal list has a large posterior tooth and 15–22 smaller teeth of rather variable size. As in *C. subedentata* sp. n. the second and third exopodite segments carry fine hairs. There is only a single short seta near the spine teeth on the inner surface of the basale compared with two setae here in *C. subedentata* sp. n. Also the three small setae at the base of the dorsal claw seta of the third exopodite segment are appreciably shorter than in *C. subedentata* sp. n.

Maxilla (Fig. 8F) and furca (Fig. 8D). As for *C. subedentata* sp. n.

Labrum (Fig. 8E). This differs from the labrum of *C. subedentata* in having only very faint lines on the hyaline plate.

Penis (Fig. 7H). There are usually six, but occasionally only five, transverse muscle bands.

Sixth limb (Fig. 7I). As in *C. subedentata* sp. n. except for the proportionally rather longer setae on the final segment (Table 4).

DESCRIPTION OF FEMALE. Carapace (Fig. 6). The carapace lengths of 31 specimens range from 1·576 mm to 1·734 mm with a mean value of 1·651 ± 0·067 mm

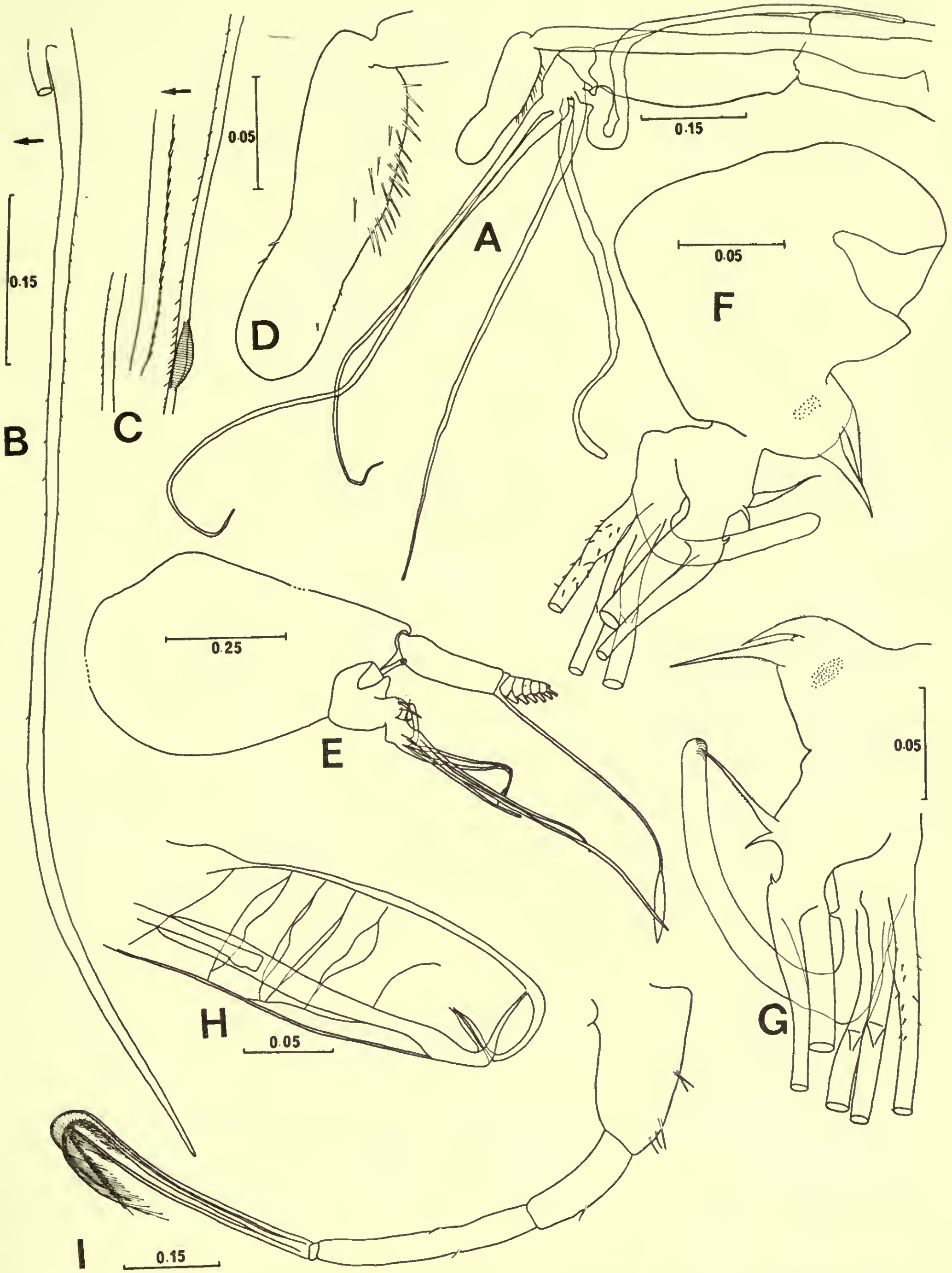
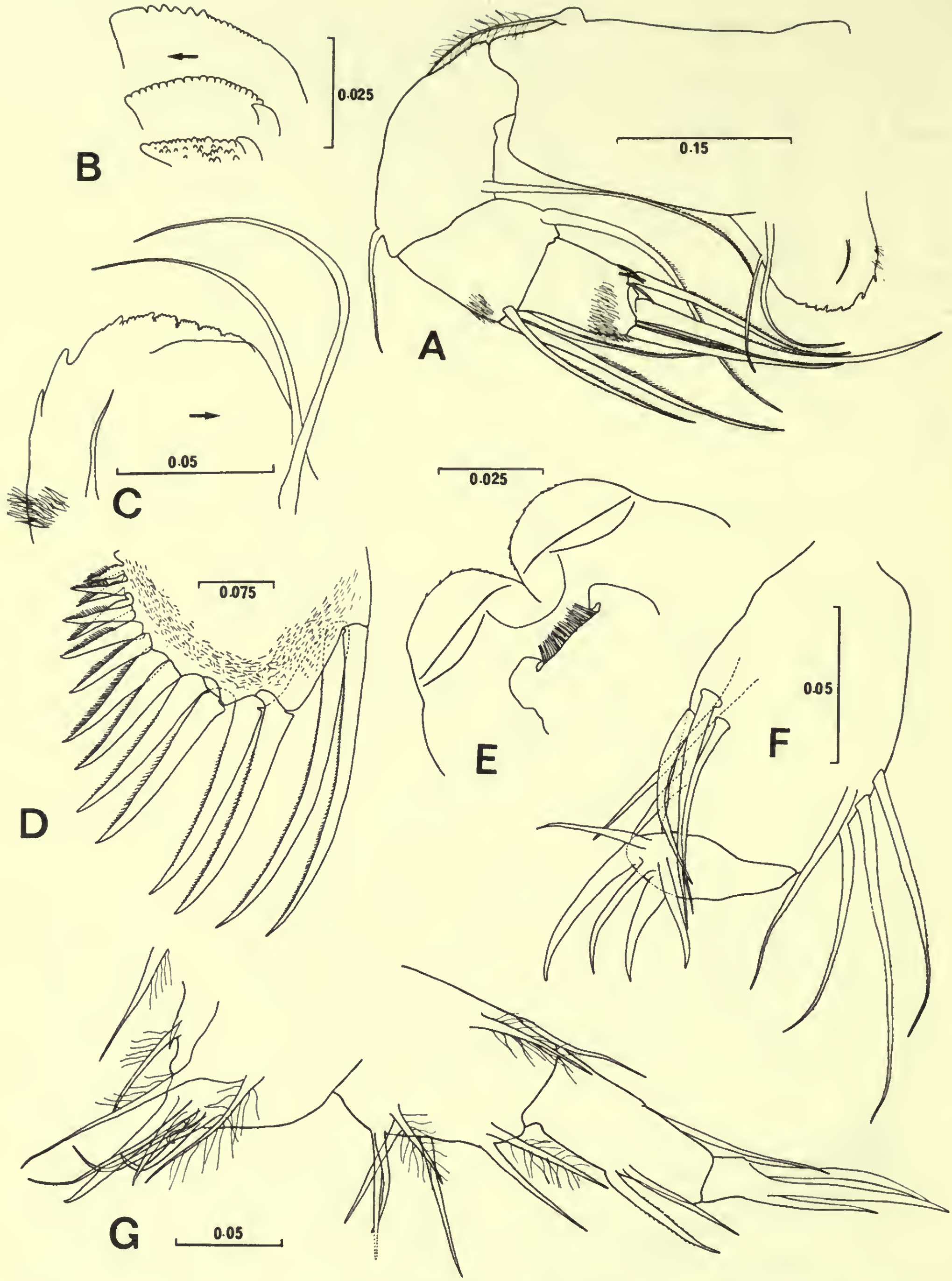


FIG. 7. Male dimorphic parts of *Conchoecia* aff. *edentata*; arrows indicate anterior. (A) First antenna and frontal organ. (B) *g* seta of second antenna. (C) Main armature of (from left to right) *d*, *e* and *b* setae of first antenna. (D) Capitulum of frontal organ. (E) Second antenna. (F) Endopodite of left second antenna. (G) Second and third segments of endopodite of right second antenna. (H) Penis. (I) Sixth limb.


B
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A
C
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0.025
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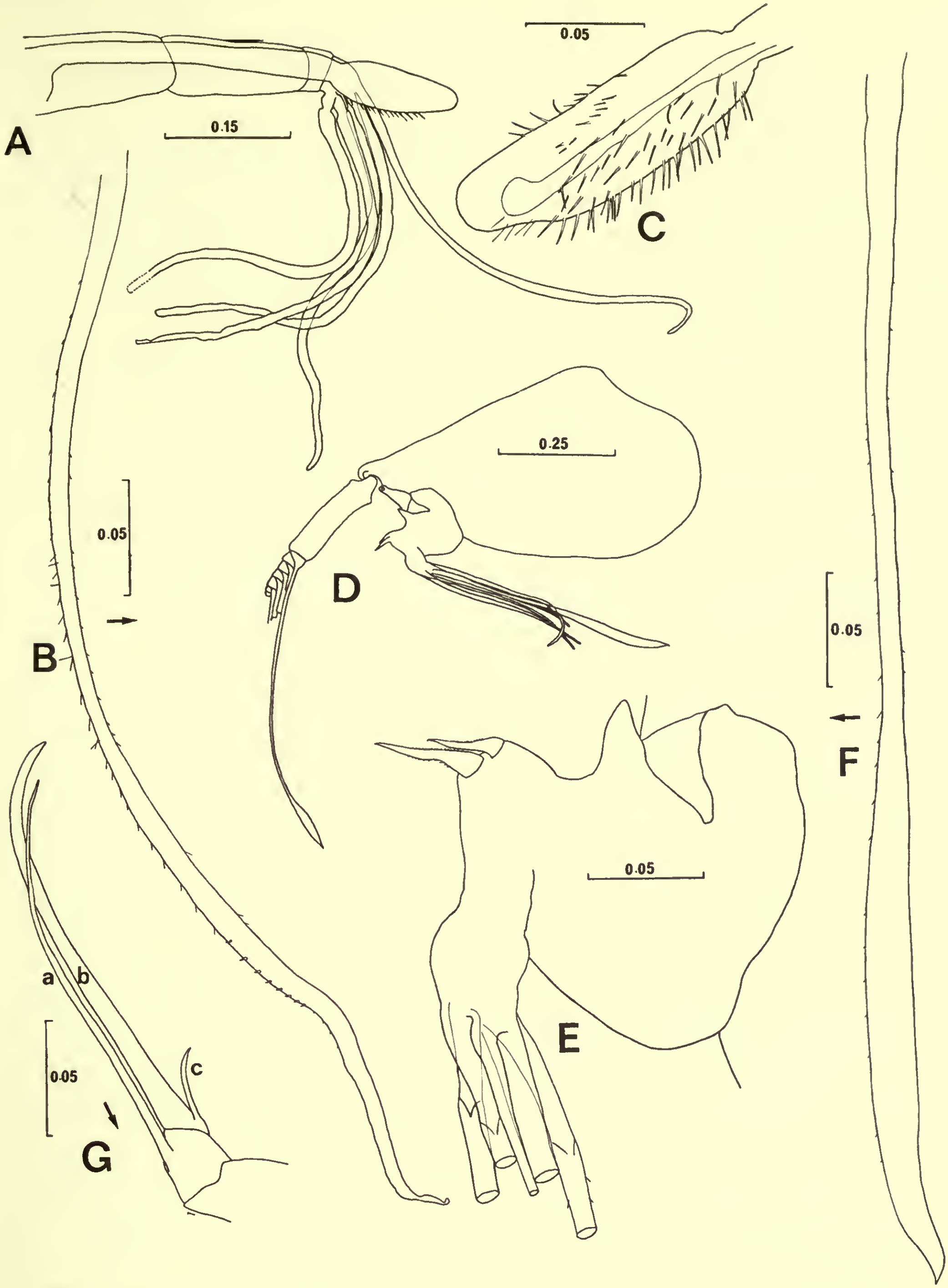
0.05
F
D
G
0.05

FIG. 8. Non-dimorphic parts of *Conchoecia* aff. *edentata*; arrows indicate anterior. (A) Basale, endopodite and exopodite of mandible. (B) From top to bottom, cutting edge, distal and proximal tooth lists of mandibular coxale. (C) Cutting edge and adjacent setae of mandibular basale. (D) Caudal furca. (E) Labrum. (F) Maxilla. (G) Fifth limb.


A
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G

Fig. 9. Female dimorphic parts of *Conchoecia* aff. *edentata*; arrows indicate anterior. (A) First antenna and frontal organ. (B) *e* seta of first antenna. (C) Capitulum of frontal organ. (D) Second antenna. (E) Endopodite of right second antenna. (F) *g* seta of second antenna. (G) Final segment and setae of sixth limb.

(Fig. 1). The lateral outline and gland positions are similar to *C. subedentata* sp. n. There is no surface ornamentation.

Frontal organ (Fig. 9C). As for *C. subedentata* sp. n.

First antenna (Figs 9A, B). As for *C. subedentata* sp. n. except that the *e* seta is proportionally longer (Table 2) and bears 36–46 posterior spines. These comprise 18–24 spines on the proximal tubular part of the seta (11–12 of these are small and difficult to distinguish), 7–10 long distally pointing spines on the distal flattened section followed by 7–9 proximally pointing spines with expanded bases and 3–5 weaker distally pointing spines.

Second antenna (Figs 9D–F). The protopodite is proportionally shorter and the *f–j* setae are proportionally rather longer than in *C. subedentata* sp. n. (Table 3). The first exopodite segment usually bears a few small scattered spines. The *f* seta has up to six small anterior spines. The distal flattened part of the *g* seta is more slender than in *C. subedentata* sp. n. On the anterior side of this seta are 19–26 spines of which the proximal 5–8 lie on the tubular part of the seta; the posterior side bears 6–8 similar spines, all on the tubular part. The *j* seta carries a few proximal spines.

Sixth limb (Fig. 9G). The ventral *a* seta is considerably shorter than in *C. subedentata* sp. n. and does not extend beyond the *b* seta. The *c* seta is about twice the proportional length of this seta in *C. subedentata* sp. n. (Table 4).

JUVENILES. Earlier (IV and V) juvenile stages of *C.* aff. *edentata* overlap in length with the corresponding stages of *C. subedentata* sp. n. and so are difficult to distinguish. The following lengths are of a few specimens which exceed the maximum size for the corresponding instar of *C. subedentata* and so probably belong to *C.* aff. *edentata* (Fig. 1): Stage IV, 0·808–0·847 mm, mean 0·827 mm (3 specimens); Stage V, 0·985–1·083 mm, mean 1·047 mm (6 specimens). Male Stage VI juveniles range from 1·162 mm to 1·300 mm, mean 1·281 (5 specimens) and females from 1·281 mm to 1·320 mm, mean 1·311 mm (7 specimens). Stage VI juveniles of *C.* aff. *edentata* are thus comparable in size to adult males and small adult females of *C. subedentata* sp. n. and so easily distinguishable from the final juvenile instars of this species.

REMARKS. This Northeast Atlantic form is at variance with Müller's original description of *C. edentata* (1906 : 76, pl. 15, figs 24–29) from the Antarctic in three important respects. (i) Müller's single adult specimen, a male, is longer (1·70 mm) than Atlantic males. (ii) The carapace of Müller's specimens has 'ziemlich auffälliger' dorsal and anterior striations, 'ungewohnlich umfangreich' asymmetrical glands and an 'umfangreiche sehr auffällige' group of gland cells in the middle of the ventral margin (Müller 1906 : 77). In contrast the *Discovery* specimens have no surface ornamentation and the glands are much smaller. (iii) The *c* seta of the first antenna is considerably longer in the *Discovery* material than in Müller's male (pl. XV, fig. 27).

There is insufficient evidence to decide whether these differences warrant separating the North Atlantic and Antarctic forms as distinct species or whether they are only intraspecific variations. Until Antarctic specimens are redescribed, it seems best to leave the nomenclature of the North Atlantic form open and assign it to *C.* aff. *edentata*.

Descriptions of *C. edentata* by later workers also differ more or less from the form described here and, like Müller's, the material of these authors was caught outside the North Atlantic. Barney (1921 : 183, 184) first described the female (from the Antarctic) and found the ventral gland to be 'less noticeable than in the male' although his fig. 5a shows it to be larger than in the *Discovery* material. Also 'the anterioventral curve [of the outline] viewed from the inside has an imbricate appearance' in Barney's specimen. Although there are no other differences, Barney's figures and descriptions are too inadequate for a meaningful comparison to be made. However, it is significant that his specimen (1·62 mm) is comparable to the mean carapace length of North Atlantic females (1·651 ± 0·067 mm).

Rudyakov (1962) records three adults and two juveniles from the Northwest Pacific. His description and figures agree well with the form described here. There are a few minor differences : Rudyakov's male has no small spines on the first exopodite segment of the male second antenna, and the *d* seta of this limb is shorter (see Rudyakov, figs 12B, G), the proximal mandibular tooth list has more teeth, there are no hairs above the spine teeth of the mandibular basale (according to Rudyakov, fig. 13B), in fig. 11G of Rudyakov the basal seta, the lateral and three posterior setae of the maxilla are shorter than in my specimens and the hyaline plate of the labrum has fewer teeth (Rudyakov, fig. 12). These differences are probably only of intraspecific significance. Of more importance are the carapace lengths of Rudyakov's adult female (1·83 mm) and two Stage VI females (1·43 and 1·45 mm) which are much greater than the corresponding lengths for the North Atlantic form, although his two adult males (lengths also 1·43 and 1·45 mm) measure close to the mean carapace length of North Atlantic males. This size difference between the females but not the males is puzzling and makes it difficult to assess the conspecificity or otherwise of the two forms.

Poulsen (1973 : 107, 108) attributes a juvenile female from the Pacific off New Caledonia to *C. edentata*. This individual differs in several respects from *C.* aff. *edentata*. It is much longer (1·50 mm) than *Discovery* Stage VI juvenile females, the dorsal seta of the first antenna is longer (Poulsen, fig. 53g) ; there are 'medium-long' hairs on the lunular bulge of the second antenna (fig. 53c) ; on the mandibular basale, the spine teeth are longer and the primary cusps of the serrated teeth are more pronounced (fig. 53d) ; the edge of the mandibular coxale lacks teeth (fig. 53d), the proximal and distal tooth lists have two large posterior teeth (fig. 53d). These differences are considerable and Poulsen's specimen probably belongs to a distinct species.

Finally Deevey (1974 : 368) records three females (1·65, 1·73 and 1·73 mm long) and two juveniles (1·40 and 1·45 mm long) from the South Atlantic. The females fall just within the size range of *C.* aff. *edentata* although the juveniles are rather larger than Stage VI specimens in the *Discovery* material. In the absence of additional details the comparison can be taken no farther. Other authors (Müller, 1908, 1912 ; Iles, 1953 ; Hillman, 1967, 1969) give no descriptions, figures or lengths.

GEOGRAPHICAL DISTRIBUTION. Müller (1906 : 76), 1♂, 1 juvenile ? ♀, Indian Ocean sector of Antarctic, 55°S ; Müller (1908 : 65), Antarctic, 61°S and Indian Ocean, 0° ; Barney (1921 : 163), 2♀ (1 juvenile), 2♂ (1 juvenile), Antarctic, 72°S, 0–1000 m ; Iles (1953 : 263), 1♀, Atlantic 23°S, 500–250 m ; Rudyakov (1962), 2♂, 3♀ (2 juvenile), Northwest Pacific, 44°N (1568–1900 m), 46°N (1190–2500 m), 49°N (580–1300 m) ; Hillman (1967, 1969), Antarctic, numerous stations between 50°S and 70°S ; Deevey (1974 : 368) 3♀, 2 juveniles, South Atlantic between 23°S and 55°S. As discussed above, most of these specimens are regarded as only questionable synonyms of *C.* aff. *edentata.*

In the Northeast Atlantic, this form was found at the following stations ; the number of specimens caught at each station is given in parentheses : Station 7709, 60°N, 20°W (37) ; Station 7711, 53°N, 20°W (21) ; Stations 7406 (18), 7478 (3), both 40°N, 20°W ; Station 7856, 30°N, 23°W (1) ; Station 7089, 18°N, 25°W (23) ; Station 6665, 11°N, 20°W (2). The depth distribution at different stations is summarized in Fig. 20.

TABLE 5

Summary of the main differences between the *edentata* and *gaussi* species groups of *Conchoecia*

	edentata group	*gaussi* group
1.	Capitulum of ♂ and ♀ frontal organ shorter (Tables 2 and 3)	–
2.	♂ and ♀ first antenna longer (Tables 2 and 3)	–
3.	Pad on *b* seta of ♂ first antenna relatively short	Pad elongate
4.	*c* seta of ♂ first antenna longer than limb (Table 2)	Short and wide
5.	*a–d* setae of ♀ first antenna longer or slightly shorter than *e* seta (Table 3)	These setae much shorter than *e* seta
6.	*e* seta of ♀ first antenna with distal, proximally directed spines	All spines point distally
7.	Dorsal seta of ♀ first antenna very short	Long and extends well beyond limb
8.	Protopodite of second antenna longer, particularly in ♂ (Tables 2 and 3)	–
9.	No hairs on protopodite	Hairs present behind endopodite
10.	*h* and *i* seta of ♀ and ♂ second antenna spineless	Spines near base
11.	*f* seta of ♂ second antenna slightly longer than *h–j* setae (Table 2)	Much longer than *h–j* setae
12.	Ventral surface of mandibular basale lacks hairs	Carries fine hairs
13.	Only one marginal seta on inside of first mandibular exopodite segment	3 additional smaller setae inside margin
14.	4 posterior setae on maxilla endopodite	6 setae
15.	Labrum with small weak teeth	Teeth larger and stronger
16.	Short distal seta on dorsal surface of first exopodite segment of fifth limb	This seta long, extending to final segment
17.	♀ sixth limb with long flexible *a* seta, claw-like *b* seta and very short *c* seta	All 3 setae are claw-like and *a* seta is shortest

gaussi group

gaussi group Skogsberg, 1920 : 676, 677.
Gaussicia Poulsen, 1973 : 103, 104 (in part).

DIAGNOSIS. Both valves with median glands ; asymmetric glands are in usual place. Male first antenna with *a* seta reaching to base of limb (*C. incisa*) or to end of first segment (*C. gaussi*) ; *c* seta is short, flat and widened with short continuation above horizontal basal stalk ; armature of *b*, *d* and *e* setae is as in *edentata* group. Dorsal seta of female first antenna is long, *a–d* setae are short. Male second antenna has blunt ended (*C. incisa*) or narrow and tapering (*C. gaussi*) *f* seta, and *g* seta is blunt ended (*C. incisa*) or slightly widened and then tapered distally (*C. gaussi*). Maxilla bears six anterior setae. Labrum with numerous large teeth. Female sixth limb carries three terminal claw setae.

REMARKS. The *gaussi* group is restricted in this paper to *C. gaussi* and *C. incisa*, the two species originally included by Skogsberg (1920). This group is probably related to the *bispinosa* group to which Müller (1906, 1908) assigned *C. incisa* and *C. gaussi*. These species, particularly *C. gaussi*, resemble typical members of the *bispinosa* group (i.e. *C. bispinosa* Claus, 1890, *C. secernenda* Vávra, 1906, *C. haddoni* Brady & Norman, 1896 and *C. striola* Müller, 1906 as redescribed by Angel, 1970 and Poulsen, 1973) in a number of the characters which were used in Table 5 to distinguish them from the *edentata* group. The main points of similarity are the short *a–d* setae and long dorsal seta of the female first antenna, the short hairs behind the endopodite on the female second antenna, the development of spines in both sexes near the bases of the *h* and *i* setae of the second antennae, the four setae on the inside of the first mandibular exopodite segment and the ventral hairs on the basale of this limb, the six anterior setae of the first endopodite segment of the maxilla, the rounded notch and well-developed teeth of the labrum, the long distal dorsal seta on the first exopodite segment of the fifth limb and the three stiff claw setae on the final segment of the female sixth limb. In addition, *C. gaussi* was described by Müller (1908) as having several enlarged gland cells near the middle of the posterior margin resembling the gland cells which he regarded as typifying the *bispinosa* group. These cells were also observed by Skogsberg (1920) in *C. gaussi* but were not visible in any *Discovery* specimens. Angel (1968b) reported that glands in this region release a bioluminescent secretion in *C. secernenda* and *C. bispinosa*.

The *gaussi* group is distinguished from the *bispinosa* group by the presence of the ventral gland, the absence of the *c* seta and the distally widened *g* seta (thin and tapered in *bispinosa* group) on the female second antenna, the shorter *c* seta of the male second antenna and the *g* seta of this limb which is tapered in the *bispinosa* group but square ended in *C. incisa* and in *C. gaussi* is widened distally before tapering and finally the absence of a terminal spine on the hook appendages (see Skogsberg, 1920 and Granata & di Caporiacco, 1949 : 12, 13). Also the *c* seta of the male first antenna is flattened and widened and extends dorsally above the basal stalk in the *gaussi* group ; this seems to be a unique feature.

Conchoecia incisa Müller, 1906
(Figs 10–14)

Conchoecia incisa Müller, 1906 : 94, pl. 19, figs 1–11 ; Müller, 1912 : 80 ; Angel, 1969 : 541 ; Poulsen, 1969 : 163, 164 ; Deevey, 1974 : 368, 369.
Conchoecia gaussi ? (Müller) Angel, 1968a : 308 (*non* Müller, 1908).

DIAGNOSIS. Species of *gaussi* group characterized by carapace length (♂ 1·822–1·911 mm, mean 1·877 ± 0·030 mm ; ♀ 2·462–2·837 mm, mean 2·644 ± 0·024 mm) and tapering lateral outline of female ; male frontal organ long and slender with long hairs, *a* seta of ♂ first antenna has lateral lobes near base and *e* seta bears 25–33 pairs of spines ; *f* and *g* setae of ♂ second antennae are square ended ; cutting edge of mandibular coxale lacks teeth.

MATERIAL. One hundred and twenty-four specimens comprising 31 females, 8 males and 85 juveniles. Dissected male and female specimens, stained with lignin pink and mounted on slides in Euparal, are deposited in the British Museum (Natural History) reg. nos 1974.751 and 752.

DESCRIPTION OF MALE. Carapace (Fig. 11). The carapace lengths of eight specimens range from 1·822 mm to 1·911 mm with a mean value of 1·877 ± 0·030 mm (Fig. 10). In lateral view the posterior margin is gently curved and joins the ventral margin at a slightly truncated posterioventral corner. The ventral margin is almost straight and converges only slightly with the dorsal margin anteriorly. In ventral view, the carapace outline does not curve evenly towards the posterior end but is chisel shaped, the sides of the carapace in the posterior $\frac{1}{3}$ or so being straight or even slightly concave. There is no surface ornamentation. The right asymmetric gland opens above $\frac{1}{3}$ of the maximum carapace height. The median ventral gland is fairly well developed.

Frontal organ (Fig. 12D). The shaft extends beyond the first antenna, and the capitulum is about $\frac{2}{3}$ the length of the shaft. The capitulum is narrow, elongate and often curves slightly forwards ; the distal $\frac{1}{4}$ is rather expanded and the end is asymmetrically rounded. The proximal $\frac{2}{3}$ of the capitulum bears long, fine hairs mainly ventrally.

First antenna (Figs 12A–C). The first segment is slightly longer than the second and the limb lacks armature. The *a* seta is rather less than twice the length of the

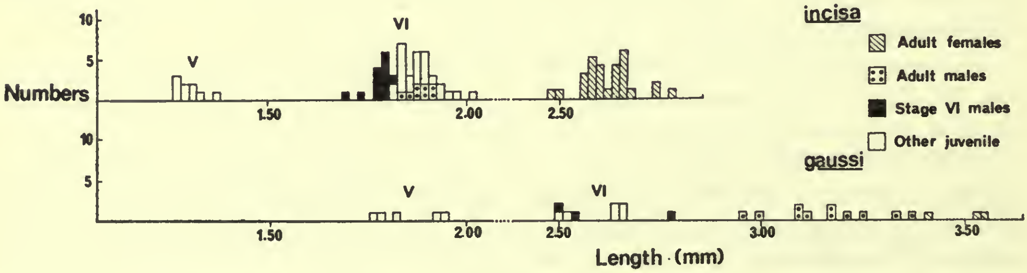

FIG. 10. Histograms showing carapace lengths of the adults and last two juvenile instars of *Conchoecia incisa* and *Conchoecia gaussi*.

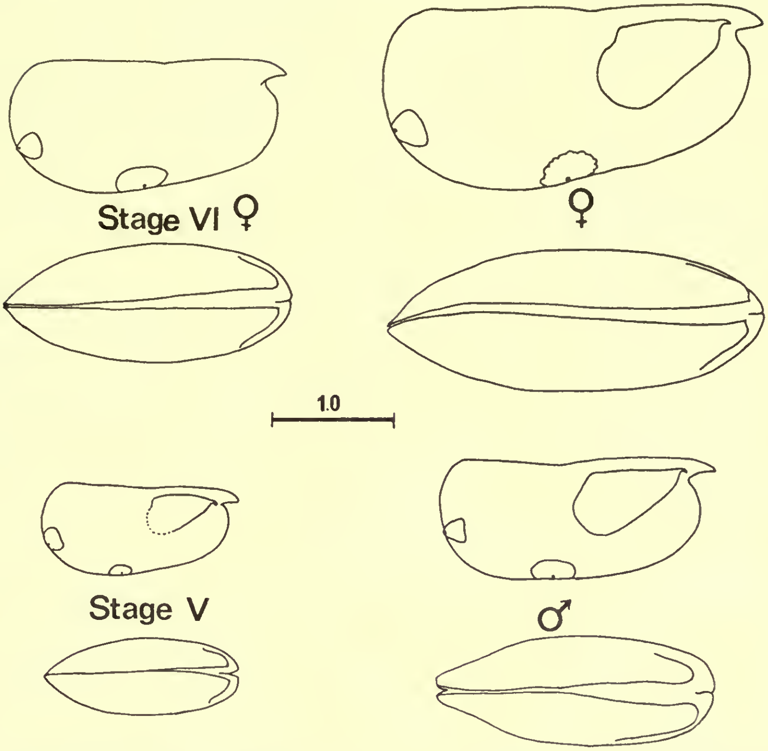

FIG. 11. *Conchoecia incisa.* Lateral and ventral carapace outlines of adults and last two juvenile instars.

limb ; proximally it loops down and up and then lies parallel to the antenna. Near its base, the *a* seta is expanded and bears side lobes, usually three dorsal and one lateral. The *b*, *d* and *e* setae are thin walled distal of their main armature. The *b* seta is rather longer than the *d* seta and carries a number of anterior spines, 4–6 are widely spaced and 7–13 closely spaced and adjacent to an elongate narrow pad ; on the thin-walled part of the seta below the pad are 8–10 smaller, closely spaced pairs of spines followed by up to 36 minute spines, usually on the anterior side. The *c* seta is short and wide with a basal horizontal stalk above which is a short dorsal continuation. The *d* seta carries 4–18 small spines usually on each side. The main *e* seta armature comprises 25–33 paired posterior spines and there may also be a few small anterior spines above the main armature.

Second antenna (Figs 12E–H). The limb has no additional armature. The processus mammillaris is conical with a terminal tubercle. The swimming setae are distally thin walled and flaccid. The *b* seta is rather more than $\frac{1}{2}$ the length of the *a* seta, the *c* seta is the same length or rather shorter than the *b* seta and the *d* seta is just under $\frac{1}{2}$ the length of the *c* seta. There are a few short hairs on the *a* and *b* setae. The *f* and *g* setae are thin walled for approximately their distal $\frac{1}{3}$ and have blunt ends, often with a filament. Both setae are bare or have 1–2 small median

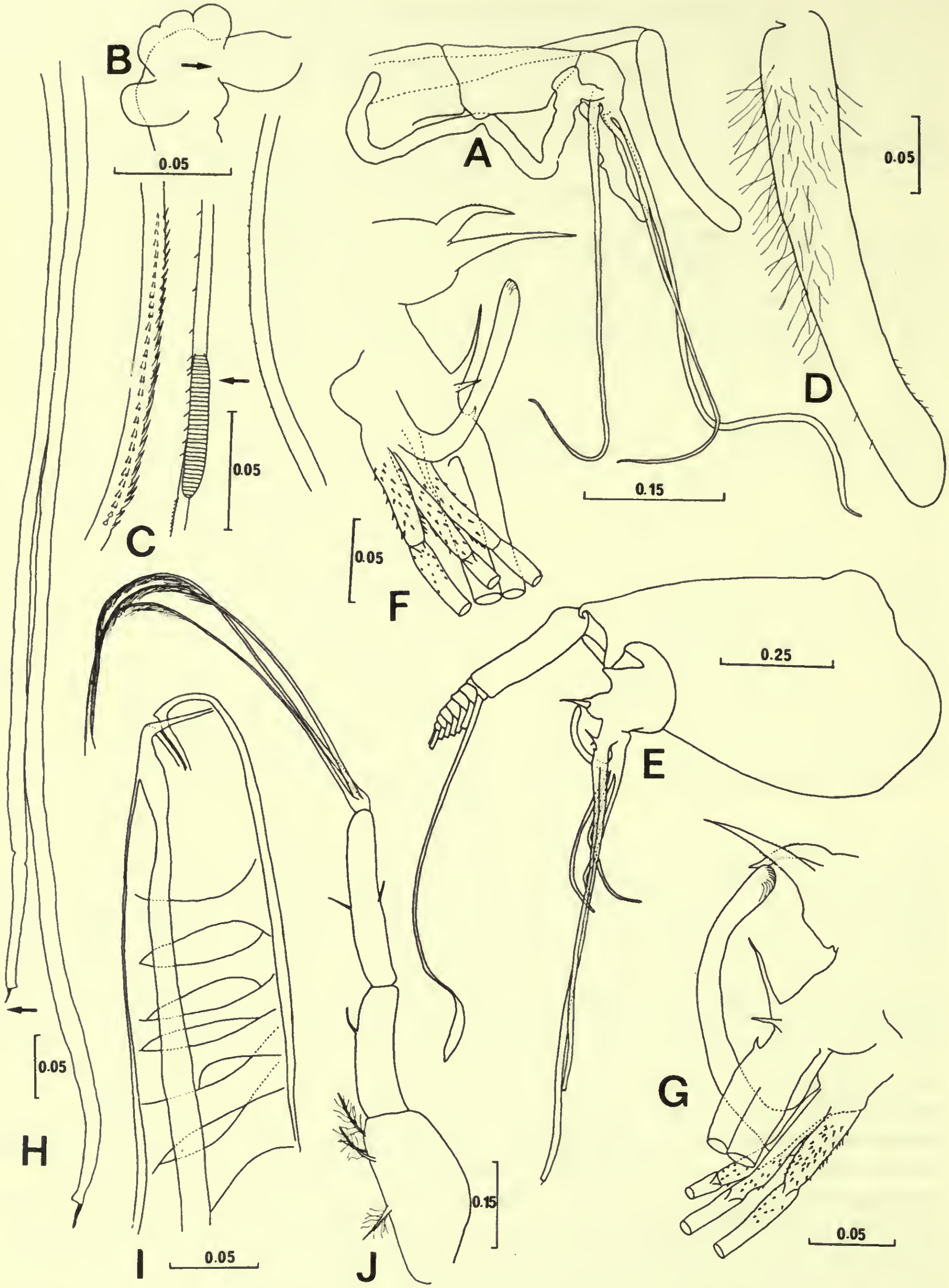

Fig. 12. Male dimorphic parts of *Conchoecia incisa* ; arrows indicate anterior. (A) First antenna and frontal organ. (B) Proximal part of *a* seta of first antenna showing lateral lobes. (C) Main armature of (from left to right) *e*, *b* and *d* setae of first antenna. (D) Capitulum of frontal organ. (E) Second antenna. (F) Second and third segments of endopodite of left second antenna. (G) Second and third segments of endopodite of right second antenna. (H) *f* and *g* setae of second antenna. (I) Penis. (J) Sixth limb.

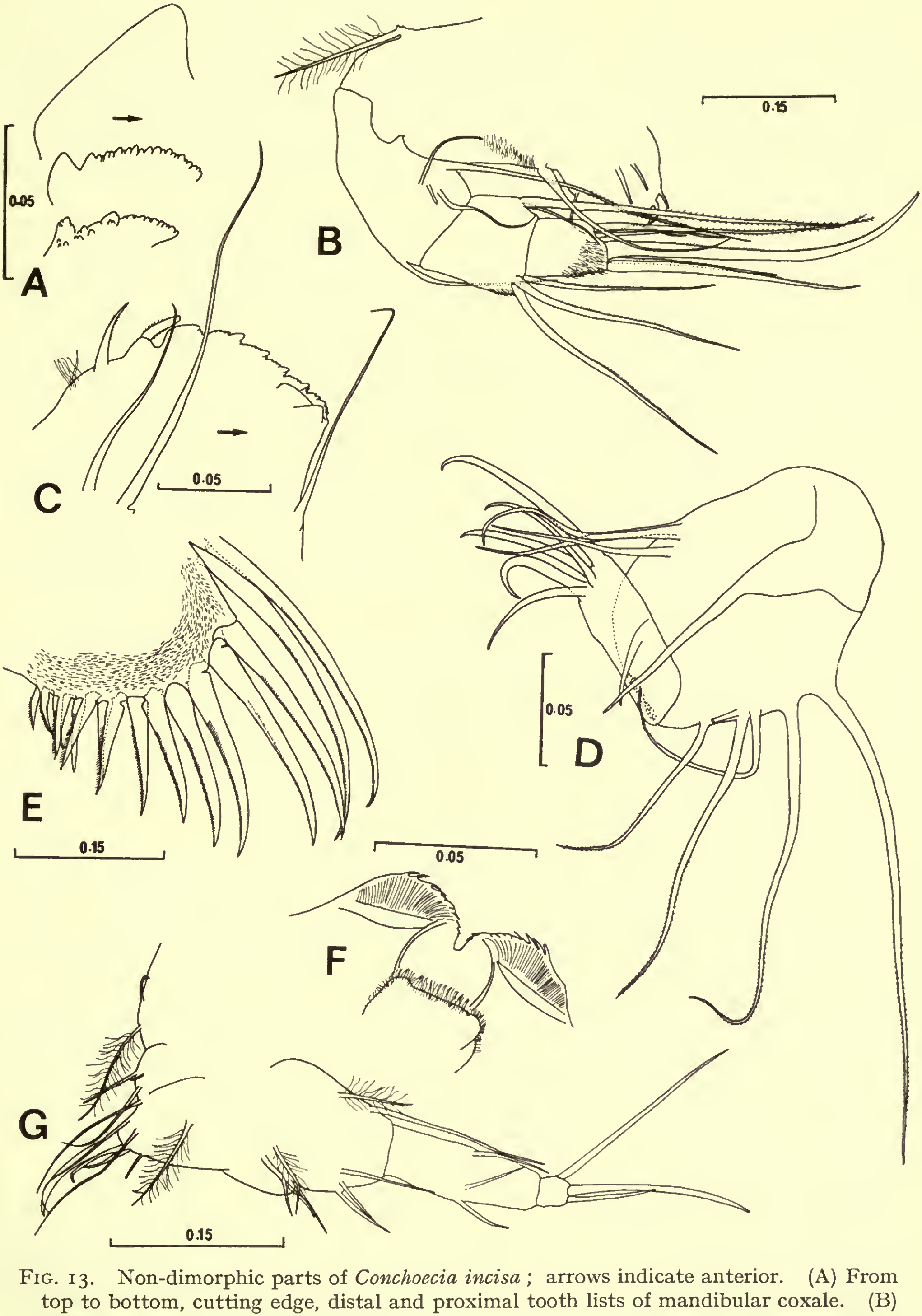

Fig. 13. Non-dimorphic parts of *Conchoecia incisa*; arrows indicate anterior. (A) From top to bottom, cutting edge, distal and proximal tooth lists of mandibular coxale. (B) Basale, endopodite and exopodite of mandible. (C) Cutting edge and adjacent setae of mandibular basale. (D) Maxilla. (E) Caudal furca. (F) Labrum. (G) Fifth limb.

spines. The *h* and *i* setae bear numerous spines above the proximal constriction while the *j* seta has rather longer spines above the constriction and a few shorter spines below. The right hook appendage has a short proximal section and a long distal section which increases in curvature towards the end where there are 9–10 subterminal ridges. The left hook appendage is smaller and has an almost straight distal section with fewer subterminal ridges.

Mandible (Figs 13A–C). The cutting edge of the coxale lacks teeth and slopes down posteriorly. On the distal tooth list is a large posterior tooth followed by (in three specimens) 17, 19 and 22 smaller teeth of rather variable size. The proximal list has a large posterior tooth and a rather smaller tooth before the mid-point; between these teeth the list slopes up and is either straight or toothed. The median tooth is followed anteriorly by (in three specimens) 12, 15 and 18 small teeth of rather variable sizes. The inner surface of the proximal list bears papillae. The cutting edge of the basale has two posterior spine teeth, one long and pointed, the other shorter and blunt, six serrated teeth and a conical inner tooth at the anterior end. The basale has a small patch of hairs above the spine teeth and a larger area on the ventral surface. There are also numerous hairs on the distal part of the third exopodite segment and a small distoventral patch of hairs on the second segment. The first exopodite segment has one long seta arising from the inner margin and three shorter setae just inside the margin.

Maxilla (Fig. 13D). The anterior margin has five setae, which decrease in size ventrally, and one shorter seta arising just inside the margin. The posterior margin has three setae and the basal seta extends beyond the end of the limb. The five setae on the final segment are long and slender. There are numerous minute spines on the bottom of the first endopodite segment.

Fifth limb (Fig. 13G). The dorsal seta of the first exopodite segment is long and extends to the final segment.

Sixth limb (Fig. 12J). This is typical for the genus.

Labrum (Fig. 13F). The hyaline membrane has four large outer teeth, 3–4 rounded teeth and 3–4 small inner teeth. The notch is rounded.

Furca (Fig. 13E). The caudal lamellae are covered with fine hairs.

Penis (Fig. 12I). The penis tapers distally. In two specimens there are six transverse muscle bands and in a third specimen, seven bands.

Description of the female. Carapace (Fig. 11). The carapace lengths of 39 specimens range from 2·462 mm to 2·837 mm with a mean value of 2·624 ± 0·062 mm (Fig. 9). The posterior margin is curved and joins the ventral margin evenly at the rather truncated posterioventral corner. The ventral margin is slightly concave or straight and converges strongly with the dorsal margin anteriorly. There is no surface ornamentation. The right asymmetric gland opens at about $\frac{1}{3}$ of the maximum shell height and the median ventral gland is fairly well developed.

Frontal organ (Fig. 14B). The shaft extends beyond the end of the first antenna and the capitulum is about $\frac{3}{4}$ the length of the shaft. The proximal $\frac{3}{4}$ of the capitulum is parallel-sided or very slightly tapered, the distal part is slightly expanded and the end is asymmetrically rounded. There are prominent ventral spines on the proximal $\frac{3}{4}$ of the capitulum and a few similar proximal spines dorsally.

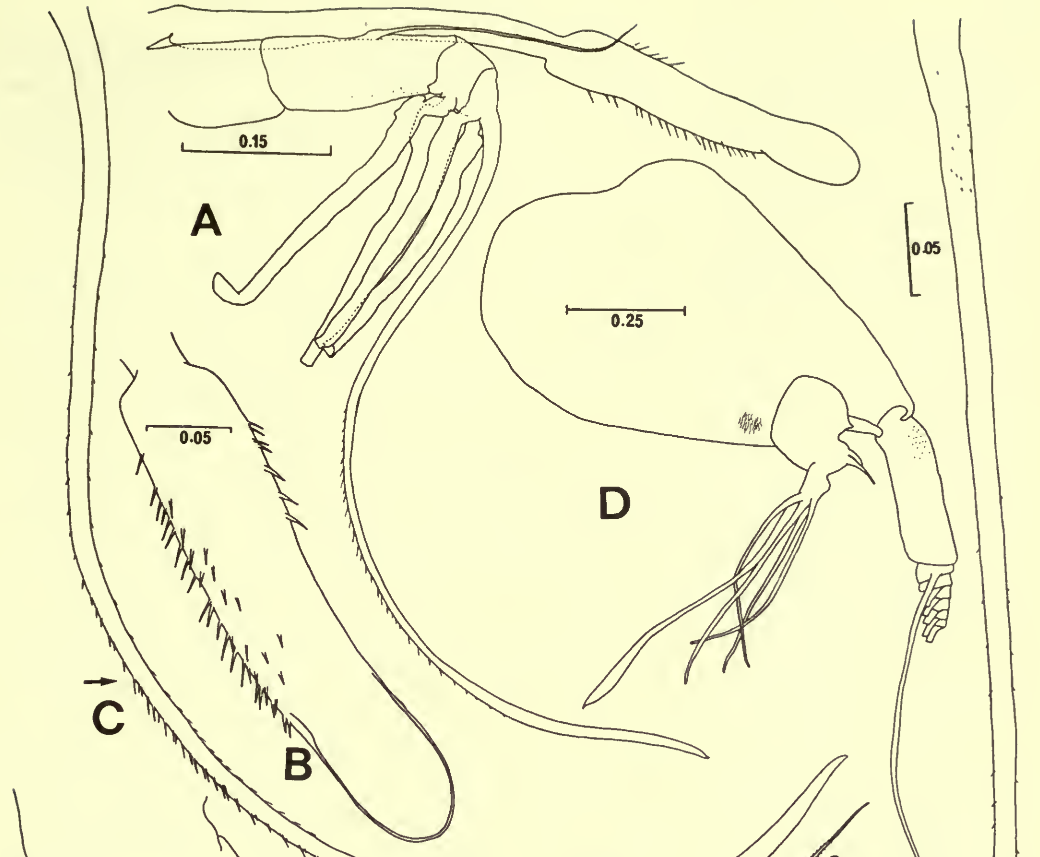
0.15
A
0.05
0.25
D
0.05
C
B
0.05
c
0.15
b
a
G
E
0.05
F

FIG. 14. Female dimorphic parts of *Conchoecia incisa*; arrows indicate anterior. (A) First antenna and frontal organ. (B) Capitulum of frontal organ. (C) *e* seta of first antenna. (D) Second antenna. (E) *g* seta of second antenna. (F) Second and third segments of endopodite of left second antenna. (G) Sixth limb.

First antenna (Figs 14A, C). The second segment is longer than the first and both have a few small ventral spines. The dorsal seta is long and armed with short hairs. The *a–d* setae are about as long as the first two limb segments combined while the *e* seta is just under three times the length of *a–d* setae and its anterior side bears 20–39 (usually 24–30) small, flat-lying hairs. On the posterior side are 16–17 small hairs, 30–35 stout spines, mostly in pairs, and 7–11 smaller spines on the distal flattened and slightly widened part of the *e* seta.

Second antenna (Figs 14D–F). The protopodite has a patch of short hairs behind the endopodite and the first exopodite segment has some small proximal outer spines. The processus mammillaris, *a* and *b* setae are as for the male. The *f* seta is rather longer than the *h–j* setae, with a number of proximal spines and 1–5 median and distal anterior spines. Proximally, the *g* seta also has a concentration of small spines. On the anterior side, these are followed by 15–19 spines of which 5–9 are on the distal flattened and widened part of the seta ; the posterior side bears 7–9 similar spines of which only 1–2, if any, are on the flattened section. Both *h* and *i* setae have numerous spines above and below the proximal constriction. The *j* seta has rather longer spines, 7–8 arising from slight 'bumps' on the inside of the seta, above the constriction.

Sixth limb (Fig. 14G). The three setae on the final segment are slender and claw-like. The dorsal *c* seta is longer than the *b* seta and rather less than twice the length of the ventral *a* seta.

JUVENILES (Fig. 11). Nine Stage V juveniles range from 1·280 mm to 1·379 mm with a mean length of 1·308 ± 0·031 mm. Male and female Stage VI juveniles are readily distinguishable ; the males are shorter (1·694–1·812 mm, mean length 1·773 ± 0·03 mm in 13 specimens) than the females (1·793–2·009 mm, mean of 1·878 ± 0·05 mm in 25 specimens). The males only increase slightly in size at the final moult while the size increase is much greater for females. Juvenile and adult lengths of *C. incisa* are summarized in Fig. 10.

REMARKS. This form differs somewhat from Müller's (1906) original description of *C. incisa* which was based on two specimens from the Indian Ocean. (i) Müller's male is larger (2·15 mm) than the North Atlantic males (1·822–1·911 mm, mean 1·877 mm) and the carapace has a much more tapered lateral outline (Müller : pl. XIV, fig. 1). On the other hand, Müller's female specimen compares well with the Atlantic form in size and outline. (ii) The original male specimen has 'wenig auffallige' surface striations although the female shell lacks ornamentation (Müller : 94). (iii) The *a* seta of the male first antenna extends only just beyond the main joint of the limb (Müller : pl. XIX, fig. 4) but at least to the base of the limb in the North Atlantic form. (iv) The *e* seta of the female first antenna seems rather shorter in Müller's female (pl. XIX, fig. 3). (v) On the second antenna, only two of the 'tube setae' (*h–j*) have basal spines in Müller's female (Müller : 94) while all three of these setae are spinose in *Discovery* females.

Apart from points (iv) and (v), which are relatively minor, Müller's description and figures of his female specimen agree well with the *Discovery* females particularly in carapace length, outline and lack of surface ornamentation. The differences between Müller's male from the Indian Ocean and the North Atlantic males are more pronounced. The degree to which the two forms differ in carapace length and outline is particularly significant and this possibly warrants a taxonomic distinction between them. They are not separated here because females from the North Atlantic closely resemble Müller's female.

Another possibility is that while the females in the *Discovery* material belong to *C. incisa*, the males are of a distinct species. This would explain the considerable size difference between the two sexes. However, it is unlikely because (i) the non-dimorphic characters of males and females are closely similar and (ii) in such a comprehensive series of samples, it is improbable that of two sympatric species, one would be represented by males alone and the other by females. The conspecificity of Müller's male with his female and with the *Discovery* material should however be regarded as somewhat questionable.

Poulsen's (1969a : 163, 164) brief description of three females of *C. incisa* from the Atlantic near the equator agrees well with *Discovery* females although his later (1973) account of this species from the Pacific, Indian and Atlantic Oceans differs in a few respects. The proximal and distal tooth lists of the mandibular coxale both have a large anterior tooth which is absent from *Discovery* specimens and the structure of the labrum is rather different. These are probably only intraspecific variations. Deevey (1974 : 368) records a single female from just south of the equator in the Atlantic ; this specimen is only just shorter than the *Discovery* females.

The juveniles and females of *C. incisa* reported by Angel (1969 : 541) are included in my material. Angel (1968a : 308) earlier tentatively identified two juveniles caught above and within the thermocline at 34°N off Morocco as *C. gaussi*. On re-examination, these proved to be Stage V juveniles of *C. incisa*.

GEOGRAPHICAL DISTRIBUTION. Müller (1906, 1912), 1♀, 1♂, Indian Ocean, 0° and 26°S ; Angel (1968a : 308), North Atlantic, 34°N, 2 juveniles ; Angel (1969 : 541), 23♀ and juveniles, North Atlantic off Canaries, 28°N ; Poulsen (1969 : 163, 164), 3♀, Atlantic, just south of equator, about 2500 m ; Poulsen (1973), 103♀, Pacific, about 32° to 9°S, Indonesian Seas, about 4° to about 23°N, Indian Ocean, about 24° to about 3°N, Atlantic, about 4° to about 38°N, most common at 1000–2500 m ; Deevey (1974 : 368), 1♀, Atlantic Ocean, 3°40'S, 30°W, 200–0 m.

In the Northeast Atlantic this species was found at the following stations ; the number of specimens at each station is given in parentheses : Station 7709, 60°N, 20°W (2) ; Station 7406, 40°N, 20°W (3) ; Stations 8263 (2) and 8270 (1), both 32°N, 27°W ; Stations 7803 (1), 7856 (37), both 30°N, 23°W ; Stations 5814 (7), 5816 (1), 5818 (9), 5819 (2), 5825 (5), 6155 (12) 6156 (10), 6164 (14), 6176 (8), 6183 (1), 6193 (1) all 28°N, 14°W ; Station 7089, 18°N, 25½°W (10). The depth distribution at different latitudes is summarized in Fig. 21.

Conchoecia gaussi Müller 1908

(Figs 10, 15–18)

Conchoecia gaussi Müller, 1908 : 71, 72, pl. IX, figs 14–16, pl. X, figs 9–12 ; Müller, 1912 : 80 ; Skogsberg, 1920 : 677–681, figs CXXIX 1–11 ; Poulsen, 1969 : 164 ; Poulsen, 1973 : 106, 107, fig. 52 ; Deevey, 1974 : 369.

Non Conchoecia gaussi ? (Müller) Angel, 1968a : 308 (= *C. incisa*).

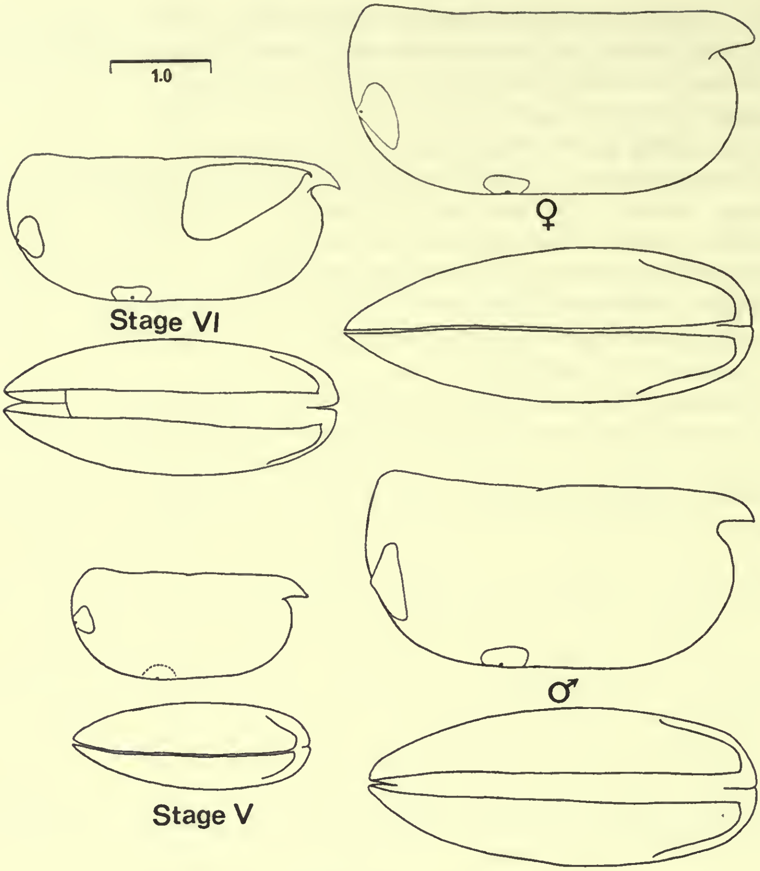

FIG. 15. *Conchoecia gaussi.* Lateral and ventral carapace outlines of adults and final two juvenile instars.

DIAGNOSIS. Species of *gaussi* group characterized by large size (♂ 2·955–3·329 mm, mean 3·138 ± 0·101 mm; ♀ 3·369–3·546 mm, mean 3·462 mm) and subrectangular lateral outline with truncated posterioventral corner; *a* seta of ♂ first antenna is shorter than limb, *b* and *d* setae are only slighter shorter than *e* seta which bears 44–49 paired spines; on ♂ second antenna, *f* and *g* setae both taper to whip-like extremities and *f* seta is only slightly shorter than *g* seta.

MATERIAL. Forty-one specimens, comprising 5 females, 12 males and 24 juveniles. Dissected male and female specimens, stained with lignin pink and mounted on slides in Euparal, are deposited in the British Museum (Natural History) reg. nos 1974.753 and 754.

DESCRIPTION OF MALE. Carapace (Fig. 15). The carapace lengths of 10 specimens range from 2·955 to 3·329 mm with a mean value of 3·138 ± 0·107 mm (Fig. 10). In lateral view the carapace is subrectangular and the dorsal margin usually curves

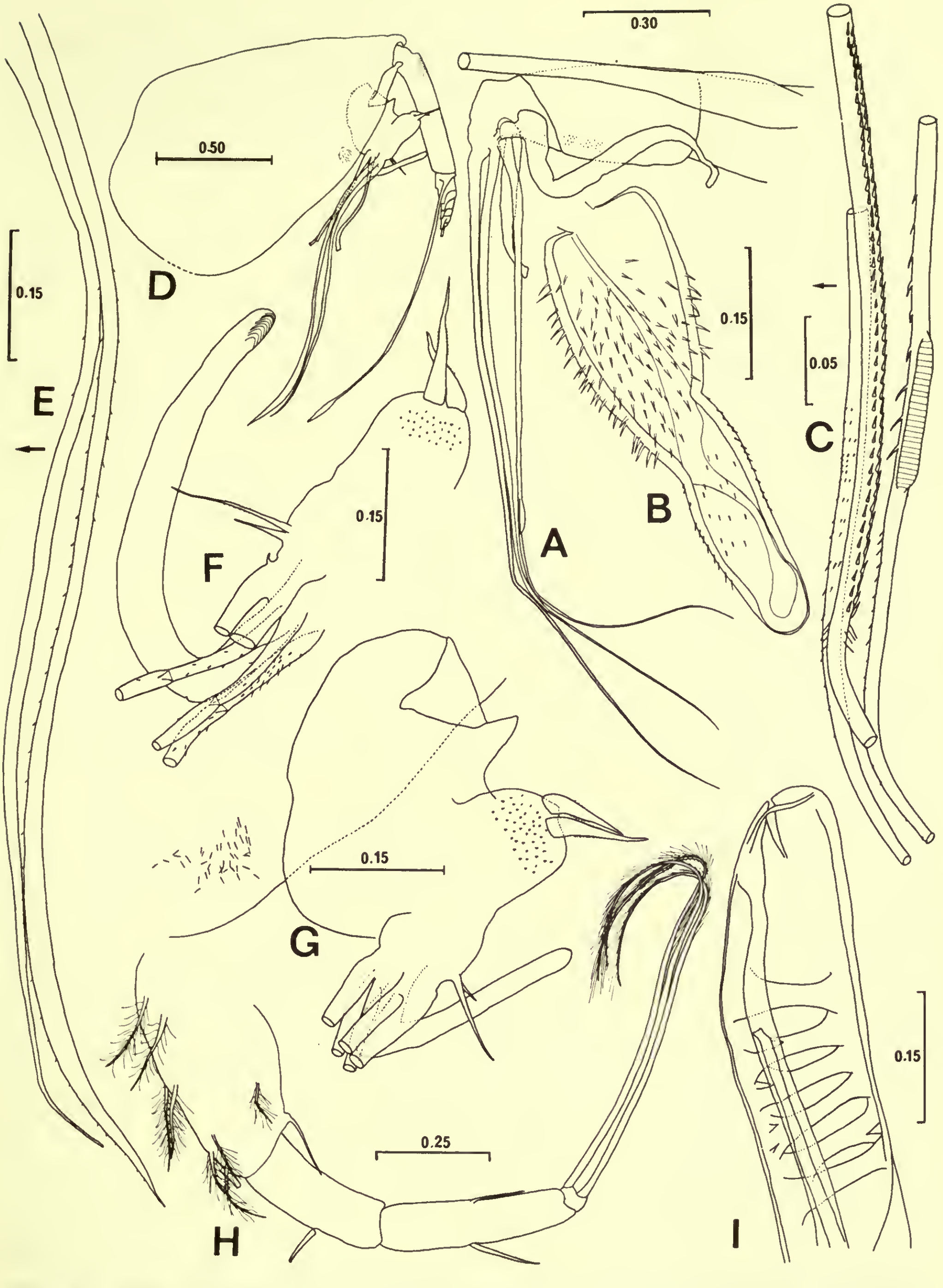
0.30
0.50
D
0.15
E
0.15
A
B
0.05
C
0.15
F
0.15
G
0.25
H
I
0.15

FIG. 16. Male dimorphic parts of *Conchoecia gaussi*; arrows indicate anterior. (A) First antenna. (B) Capitulum of frontal organ. (C) Main armature of (from left to right) *d*, *e* and *b* setae of first antenna. (D) Second antenna. (E) *f* and *g* setae of second antenna. (F) Second and third segments of endopodite of right second antenna. (G) Endopodite of left second antenna. (H) Sixth limb. (I) Penis.

upwards towards the posterior end. The posterior margin is vertical, slightly curved in the upper part and truncated posterioventrally where it joins the ventral margin evenly; the ventral margin is straight or very slightly concave and parallel to the dorsal margin. There is no surface ornamentation. The right asymmetric gland opens just about $\frac{1}{3}$ of the maximum shell height and is larger than the ventral gland which discharges behind $\frac{1}{2}$ the carapace length.

Frontal organ (Fig. 16B). The shaft extends beyond the end of the first antenna. The capitulum is strongly tapered proximally and almost parallel-sided distally, usually with a distinct angle between the dorsal edges of the two sections. Proximally, the capitulum has numerous strong closely spaced spines, the distal section bears much smaller spines.

First antenna (Figs 16A, C). The second segment is longer than the first and often carries numerous small anterioventral spines decreasing in size ventrally. The *a* seta is shorter than the limb and somewhat expanded beyond the short horizontal basal stalk. It S-bends before extending back to just past the main joint. The *b* seta is usually rather shorter than the *d* seta and has a narrow elongate pad at about $\frac{2}{3}$ of its length. On its anterior side the *b* seta bears 17–22 spines, 8–12 are closely spaced and below the pad and the remainder larger and more proximal, those adjacent to the pad being particularly large and prominent. There may also be some minute spines on the distal, thin-walled part of this seta. The *c* seta resembles that of *C. incisa.* The *d* seta has 15–20 anterior pairs of spines which increase in size distally and may be followed by minute spines like those on the *b* seta. Both *b* and *c* setae are only slightly shorter than the *e* seta (Table 2). The main *e* seta armature comprises 44–49 large paired spines, preceded by 14–23 small anterior spines and followed by 4–5 long stiff spines on both sides of the bend below the main armature.

Second antenna (Figs 16D–G). The protopodite has a patch of large hairs behind the first endopodite segment. The first exopodite segment has numerous very fine proximal spines on its anterior (outer) surface and the first endopodite segment has similar spines on the process which carries the *a* and *b* setae. The processus mammillaris is narrow and triangular. The *a* seta is 1·5–1·6 times the length of the *b* seta; the *c* seta is slender and rather longer than the *a* seta, the *d* seta is just over $\frac{1}{3}$ the length of the *c* seta; the *e* seta is a short proximally directed spine less than $\frac{1}{2}$ the length of the *d* seta. The *a–c* setae bear short hairs. The *f* seta is somewhat shorter than the *g* seta and thin walled for $\frac{2}{3}$ or so of its length. In the median part it is widened slightly and then tapers distally to a point; the *f* seta is bare or has 1–2 anterior spines in the proximal $\frac{1}{3}$. The *g* seta is thin walled and widened into a lancet shape in the distal $\frac{1}{3}$. On the posterior side are 9–10 small proximal spines and the anterior side bears 33–38 spines of which 13–16 lie on the proximal tubular part and 20–24 on the distal widened part of the seta. The *h* and *i* setae have scattered spines above the proximal constriction and sometimes a few spines below; the *f* seta has numerous rather larger spines above the constriction and scattered spines beyond this point. The proximal section of the right hook appendage is more than $\frac{1}{2}$ the length of the gently curved distal section; the angle between the two sections is less than 90° and there are 8–9 subterminal ridges. The

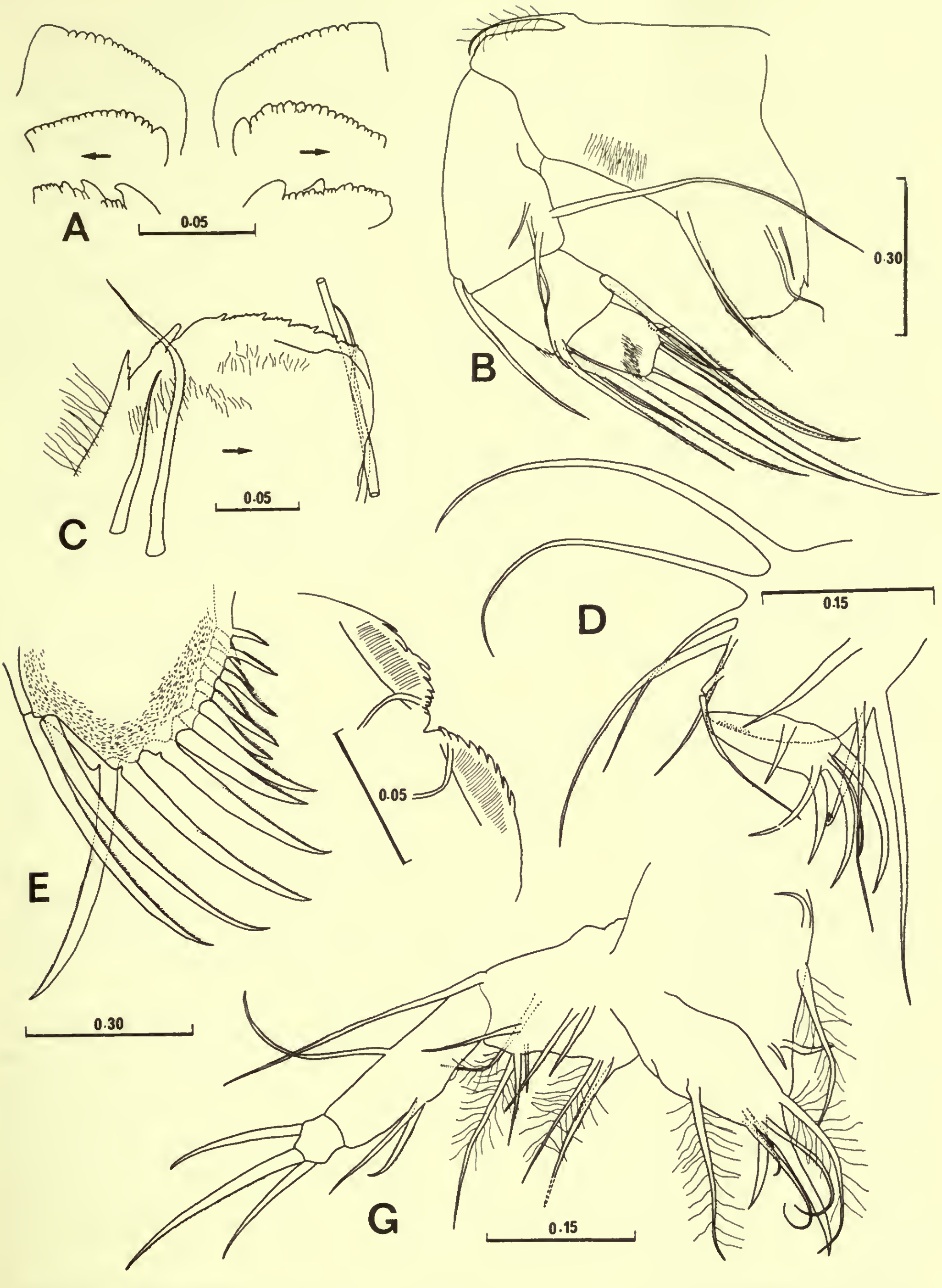

FIG. 17. Non-dimorphic parts of *Conchoecia gaussi*; arrows indicate anterior. (A) From top to bottom, cutting edges, distal and proximal tooth lists of two specimens. (B) Basale, endopodite and exopodite of mandible. (C) Cutting edge and adjacent setae of mandibular basale. (D) Maxilla. (E) Caudal furca. (F) Labrum. (G) Fifth limb.

left hook appendage has a basal angle of about 45° and a long straight distal section.

Mandible (Figs 17A–C). The cutting edge of the coxale carries 17–18 teeth, decreasing in size posteriorly, and is straight near both ends. The proximal tooth list has a large pointed posterior tooth, followed by 4–5 smaller teeth, a second large pointed tooth and 10–12 smaller anterior teeth of rather variable size. The distal list has a rather rounded posterior tooth and 19–21 smaller teeth also of variable size. The cutting edge of the basale has the usual structure; the inner tooth is broad and raised into a small central point. The basale has an area of hairs extending from the posterior margin above the spine teeth as far as the broad inner tooth. There are also numerous hairs above the ventral margin of the basale, on the distal part of the third exopodite segment and a few hairs on the outer distal edge of the second segment. The first exopodite segment bears one long marginal inner seta and three smaller setae arising inside the margin and decreasing in size proximally.

Maxilla (Fig. 17D). The first endopodite segment bears five anterior marginal setae, one seta just inside the anterior margin, three posterior marginal setae and a lateral seta. The basal seta extends to near or just beyond the end of the limb.

Fifth limb (Fig. 17G). As for *C. incisa.*

Sixth limb (Fig. 16H). As for genus.

Labrum (Fig. 17F). The hyaline plate bears 9–10 prominent teeth and the notch is V-shaped and fairly deep.

Caudal furca (Fig. 17E). The caudal lamellae are covered with fine hairs.

Penis (Fig. 16I). Slender and distally tapered with six transverse muscle bands.

DESCRIPTION OF FEMALE. Carapace (Fig. 15). The carapace lengths of four specimens range from 3·369 mm to 3·546 mm with a mean value of 3·462 mm (Fig. 10). Gland positions and lateral outline are as for the male except that the outline is rather more elongated and tapers slightly towards the anterior end.

Frontal organ (Fig. 18C). The shaft extends beyond the first antenna. The capitulum is elongate and tapers anteriorly, the proximal $\frac{1}{3}$ is rather expanded. Along the proximal $\frac{2}{3}$ to $\frac{3}{4}$ of the ventral surface are numerous strong spines; there are similar spines on the proximal $\frac{1}{4}$ to $\frac{1}{3}$ of the dorsal surface but only a few scattered lateral spines. Distally the capitulum bears much smaller spines.

First antenna (Figs 18A, B). The first segment has a few small distal spines on the ventral surface and is shorter than the second segment which carries numerous small ventral spines. The dorsal seta is as long as the first two limb segments. The *e* seta is less than twice the length of the *a–d* setae and is flattened and widened distally. It bears numerous spines which start on both sides near the base and are most concentrated and prominent near the middle of the seta. On the anterior surface are 80–100 spines which do not extend far onto the distal section of the seta, while posteriorly there are at least 130–140 spines extending onto the widened part. The spines are arranged in at least two rows for much of their extent.

Second antenna (Figs 18D–G). The *a* and *b* setae and the armature of the protopodite, the first exopodite and endopodite segments are as for the male. The *f* seta is rather more than $\frac{3}{4}$ the length of the *g* seta and bears fairly numerous basal anterior spines. The *g* seta has 7–10 rather larger basal, anterior spines followed by 28–40

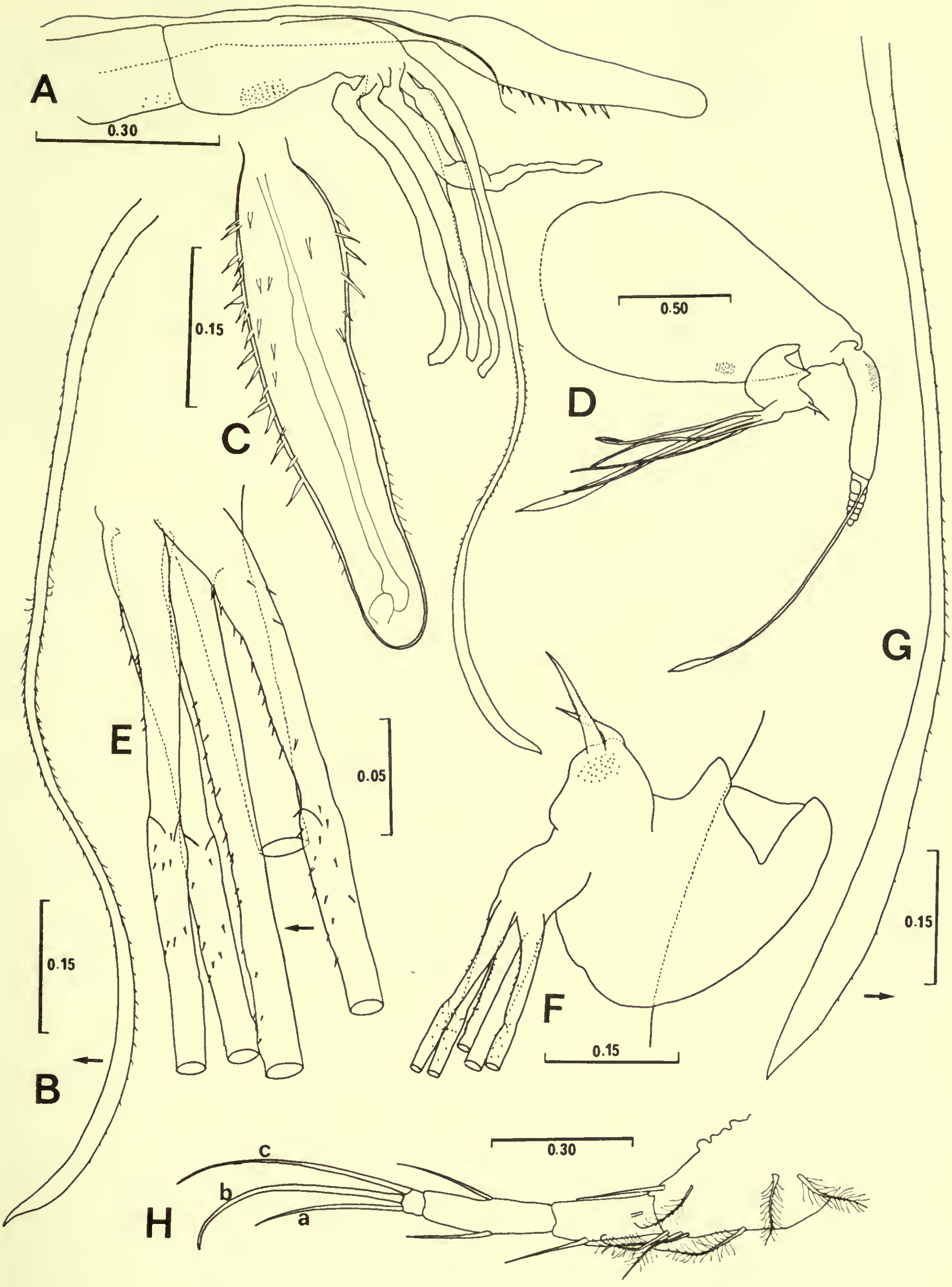
A
0.30
0.15
C
0.50
D
G
E
0.05
0.15
0.15
B
F
0.15
c
b
a
H
0.30

FIG. 18. Female dimorphic parts of *Conchoecia gaussi*; arrows indicate anterior. (A) First antenna and frontal organ. (B) *e* seta of first antenna. (C) Capitulum of frontal organ. (D) Second antenna. (E) Armature on proximal parts of *f–j* setae of second antenna. (F) Endopodite of right second antenna. (G) *g* seta of second antennae. (H) Sixth limb.

anterior spines of which 12–18 lie on the distal flattened part; there are no posterior spines on the *g* seta. The *h* and *i* setae are rather longer than the *f* seta and have scattered spines above and below the proximal constriction. The *j* seta has rather more spines above and below the constriction.

Sixth limb (Fig. 18H). The three setae on the final segment are slender and claw-like. The dorsal *c* seta is slightly longer than the *b* seta and the ventral *a* seta is about $\frac{2}{3}$ the length of the *b* seta.

JUVENILES (Fig. 15). Five Stage V juveniles range in length from 1·753 mm to 1·931 mm (mean 1·836 mm). Seven female Stage VI instars measure 2·502 mm to 2·719 mm long (mean 2·620 mm) and three male Stage VI instars have lengths of 2·778 mm, 2·541 mm and 2·502 mm. The Stage V and VI instars of *C. gaussi* are thus the same size as Stage VI juvenile females and adult females respectively of *C. incisa*. However, juvenile instars of the two species can be distinguished by their characteristic and differing outlines. Adult and juvenile lengths for *C. gaussi* are summarized in a histogram (Fig. 10).

REMARKS. The *Discovery* material is closely similar to the male described by Müller (1908 : 71–72) and the female of Skogsberg (1920 : 677–681). There are only a few differences. (i) The posterioventral corner of Müller's specimen (pl. X, fig. 9) is less truncated and more rightangular than in North Atlantic males. (ii) The carapace of Müller's specimen bears dorsal and anterior striations. (iii) There are more teeth on the cutting edge of the mandibular coxa figured by Skogsberg (fig. CXXIX 6) and the teeth have a greater size range than in the *Discovery* specimens. (iv) Skogsberg noted that the joints of the female first antenna are 'smooth' and so presumably lack the small spines present in the North Atlantic material. These differences are minor and the *Discovery* material is undoubtedly conspecific with that of Müller and Skogsberg.

Rudyakov (1962) has described the female of *C. gaussi curilensis*, a new subspecies from the Northwest Pacific, characterized mainly by its large size (4·08–4·18 mm). Two females reported by Poulsen (1969a : 164) from the South Atlantic are almost comparable in size (4·0 mm) to Rudyakov's subspecies and Poulsen's male specimen is also larger (3·30 mm) than *Discovery* males. Size seems to be an important taxonomic character in halocyprids, so this large form may be a new species rather than just a subspecies. It is also conceivable (although unlikely) that it belongs to a second adult instar of *C. gaussi* similar to the large specimens of *Gigantocypris agassizi* Müller reported by Poulsen (1962 : 34 and Table 4, p. 54; see also Angel, 1970 : 164).

Poulsen (1973 : 106) described a male and two females of *C. gaussi* from the Pacific which agree well in size and other characteristics with the North Atlantic material. Recently Deevey (1974 : 369) has reported two female specimens from the South Atlantic one of which is comparable in size to *Discovery* females (3·45 mm) and the other rather larger (3·85 mm). As noted above the two juveniles of *C. gaussi* ? reported by Angel (1968a : 308) are juveniles of *C. incisa*.

Apart from its larger size and dissimilar carapace outline, *C. gaussi* differs from *C. incisa* as follows. (i) The capitulum of the male frontal organ is shorter, broader and a different shape in *C. gaussi* and is armed with spines rather than long hairs as in *C. incisa.* (ii) The *a* seta of the male first antenna is shorter than the limb in *C. gaussi* but longer than the limb in *C. incisa* (Table 2), where it also bears lateral lobes near the base. (iii) The *b* and *d* setae of this limb are proportionally much longer in *C. gaussi* and are almost as long as the *e* seta (Table 2). (iv) The *e* seta of the female first antenna is proportionally longer in *C. gaussi* (Table 3). (v) The first exopodite segment of the male and female second antennae and the protopodite of the female second antenna are proportionally longer in *C. gaussi* (Tables 2 and 3). (vi) The swimming setae of the male second antenna are proportionally longer in *C. incisa* (Table 2) and the distal flattened part is thinner walled and more flaccid than that of *C. incisa.* (vii) In *C. gaussi* the *f* and *g* setae of this limb both taper to whip-like extremities while those of *C. incisa* are square-ended. Also the *g* seta is proportionally much shorter in *C. gaussi* and only slightly longer than the *f* seta. (viii) The *c* seta of this limb is more slender and proportionally longer in *C. gaussi.* (ix) The *h–j* setae of the male and female second antennae are proportionally much shorter in *C. incisa* (Table 2). (x) In *C. gaussi,* the cutting edge of the mandibular coxale is toothed, but in *C. incisa* it lacks teeth.

The Antarctic species *C. hettacra* Müller, 1906 is remarkably similar in outline to *C. gaussi,* particularly in the male. However, this species is smaller, the female has a rather more tapered outline and the prominent right asymmetric gland opens much further down, on the posterioventral corner.

GEOGRAPHICAL DISTRIBUTION. Müller (1908 : 72), 1♂, South Atlantic, 35°S, 2°E ; Skogsberg (1920 : 681), 1♀, South Atlantic 50°S, 50°W, 2700–0 m ; Poulsen (1969 : 164), 2♀, 1♂, Atlantic, 6°35′S (725 m) and 2°S (2500 m) ; Poulsen (1973 : 106), 1♂, 2♀, near New Guinea, about 9°S, off New Zealand, about 35°S ; Deevey (1974 : 369), 2♀, South Atlantic, 32°30′S, 750 m wire, 51°30′S, 3000 m wire.

In the Northeast Atlantic *C. gaussi* was found at the following stations ; the number of specimens at each station is given in parentheses : Station 7709, 60°N, 20°W (8) ; Station 7711, 53°N, 20°W (24) ; Stations 7482 (1), 7406 (4), both 40°N, 20°W ; Station 7856, 30°N, 23°W (2) ; Stations 7089, 18°N, 25°W (3) ; Station 6674, 11°N, 21½°W (1). The depth distribution at different latitudes is summarized in Fig. 22.

ECOLOGY

The vertical distributions of the four species described here at different latitudes in the Northeast Atlantic are shown in Figs 19–22. These sections include only data from stations where the top 2000 m of the water column was comprehensively sampled with the RMT 1+8. Angel & Fasham (1975) have analysed associations of ostracod species in this region.

Conchoecia subedentata sp. n. (Fig. 19) is a high-latitude species which is more abundant at the most northerly station sampled (60°N). It becomes steadily less common southwards and is very rare at 18°N and absent at 11°N. This species was caught mainly between 300 m and 900 m but was never present in the top 200 m and only occasionally taken below 100 m. There is a slight tendency for *C.*

subedentata sp. n. to live deeper further south. *C.* aff. *edentata* has a similar geographic distribution and is also commonest at 60°N, although there is a secondary peak of abundance at 18°N (Fig. 20). This species was usually caught at greater depths than *C. subedentata* sp. n. It was never present above 400 m and occurred most frequently below 800 m. In neither species of the *edentata* group is there any evidence for diurnal vertical migrations.

The two species of the *gaussi* group tend to occur further south; *C. gaussi* is most abundant at 53°N, and *C. incisa* at 30°N (Figs 21, 22). The vertical distribution of *C. incisa* is rather anomalous. Males are rare and none was caught above 1250 m. The females and juveniles tend to be rather shallower (below 800 m) but may sometimes be taken quite near the surface. This was particularly true at 28°N where

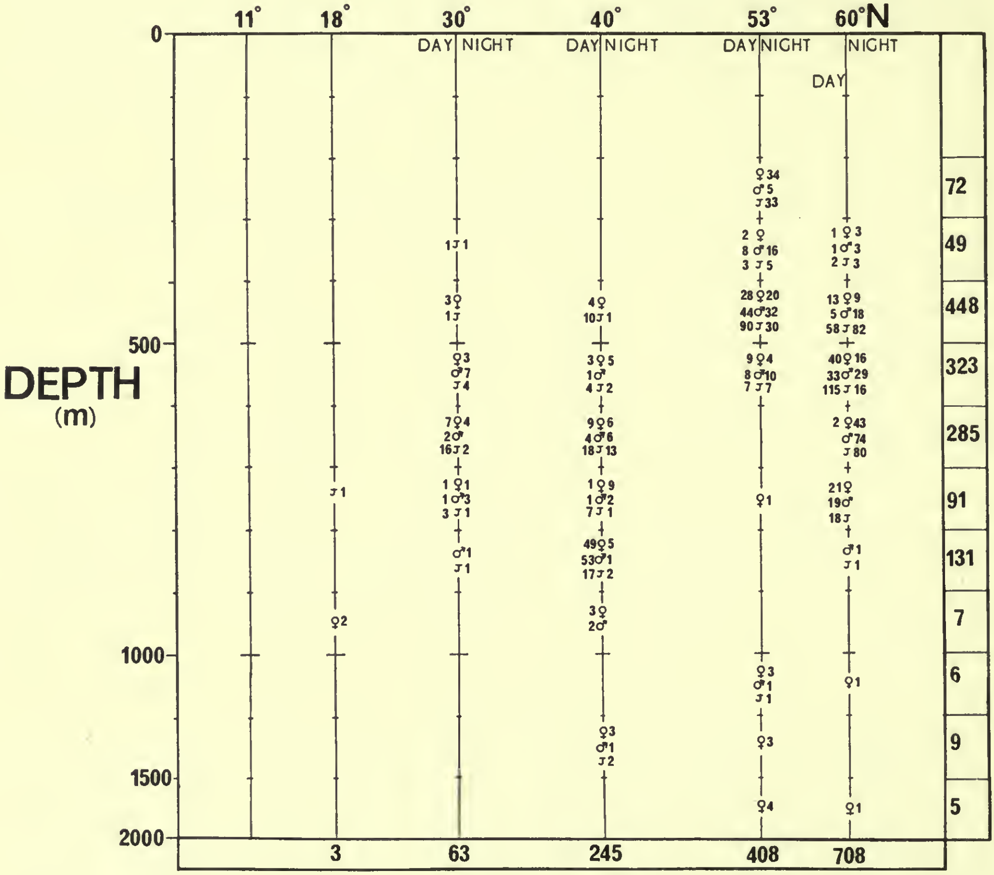

FIG. 19. *Conchoecia subedentata* sp. n. Depth distribution at various latitudes in the Northeast Atlantic Ocean. The number of males, females and juveniles caught with the RMT 1 + 8 during day and night in 100 m horizons down to 1000 m and wider horizons between 1000 m and 2000 m are shown. The figures along the bottom of the diagram are the total numbers of specimens occurring at each latitude and the figures in the right-hand column give the total numbers of specimens caught in each depth horizon.

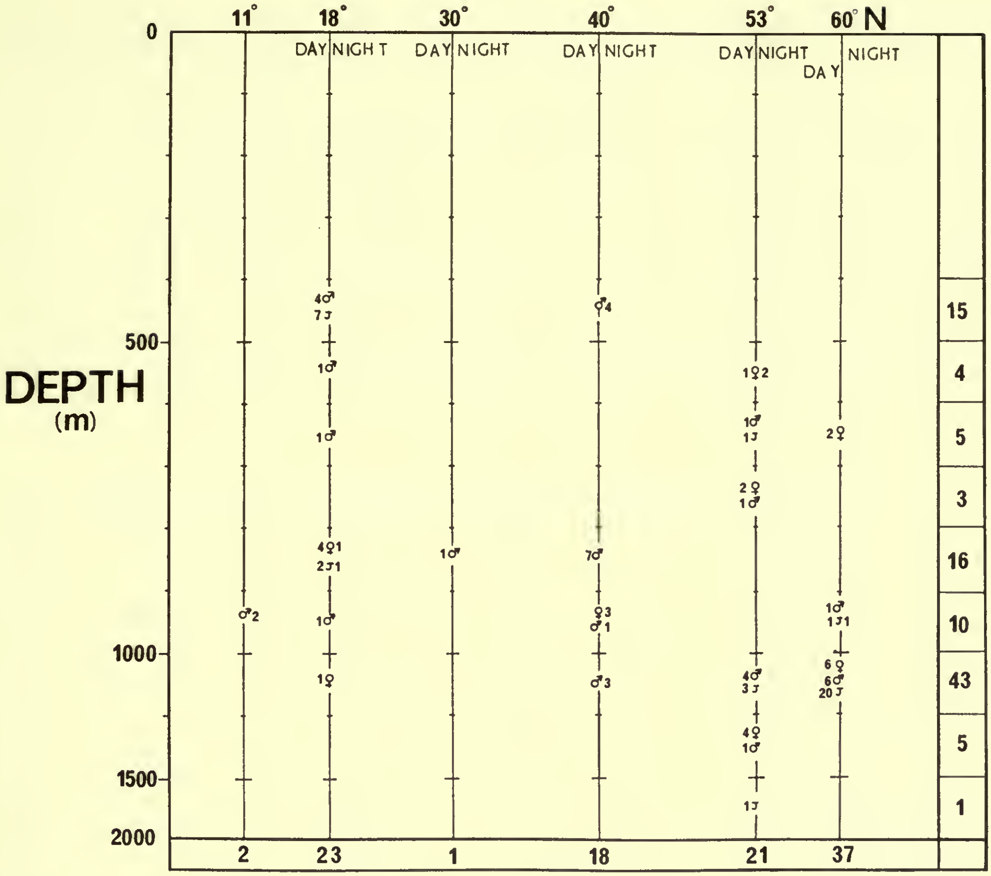

FIG. 20. *Conchoecia* aff. *edentata*. Depth distribution at various latitudes in the Northeast Atlantic Ocean. For explanation see Fig. 19.

TABLE 6

Vertical distribution during the day and night of females and juveniles of *Conchoecia incisa* at 28°N

DEPTH (m)	DAY		NIGHT	
	FEMALES	JUVENILES	FEMALES	JUVENILES
0–100			1	3
100–200		1	1	7
200–300				
300–400				1
400–500		7		
500–600	3	41		
600–700				
700–800	1	1		
800–900				2

most females and juveniles were caught between 600 m and the surface with a concentration of juveniles at 500–600 m (Table 4: these data were obtained from N113 catches and are not comparable with the data in Fig. 21 which are based on RMT 1+8 samples). This vertical distribution pattern resembles that of *Halocypris globosa* Claus, 1874. Here the males are deep-living while the females and juveniles have a bimodal distribution with peaks of abundance between 1500 m and 3000 m and in the top 100 m (Poulsen, 1969b: 49, 60). Almost all specimens of *C. incisa* caught near the surface (0–200 m) were taken at night (Table 4 and Fig. 21) which suggests that shallower members of this species migrate diurnally. However, there is no evidence for diurnal migrations by individuals living below 1000 m (Fig. 21).

C. gaussi occurs mainly below 1000 m although a few specimens were caught at shallower depths and a juvenile was obtained from the top 100 m at 53°N (Fig. 22). This species does not seem to migrate vertically although the evidence is sparse.

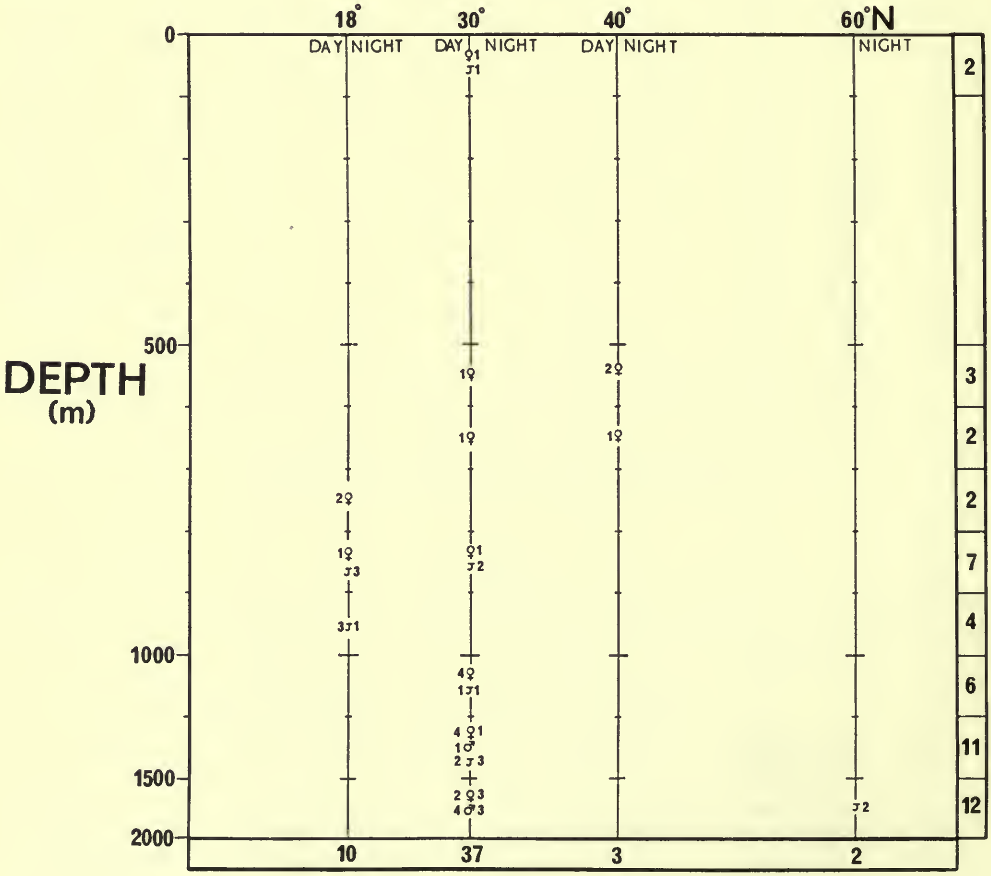

FIG. 21. *Conchoecia incisa.* Depth distribution at various latitudes in the Northeast Atlantic Ocean. For explanation see Fig. 19.

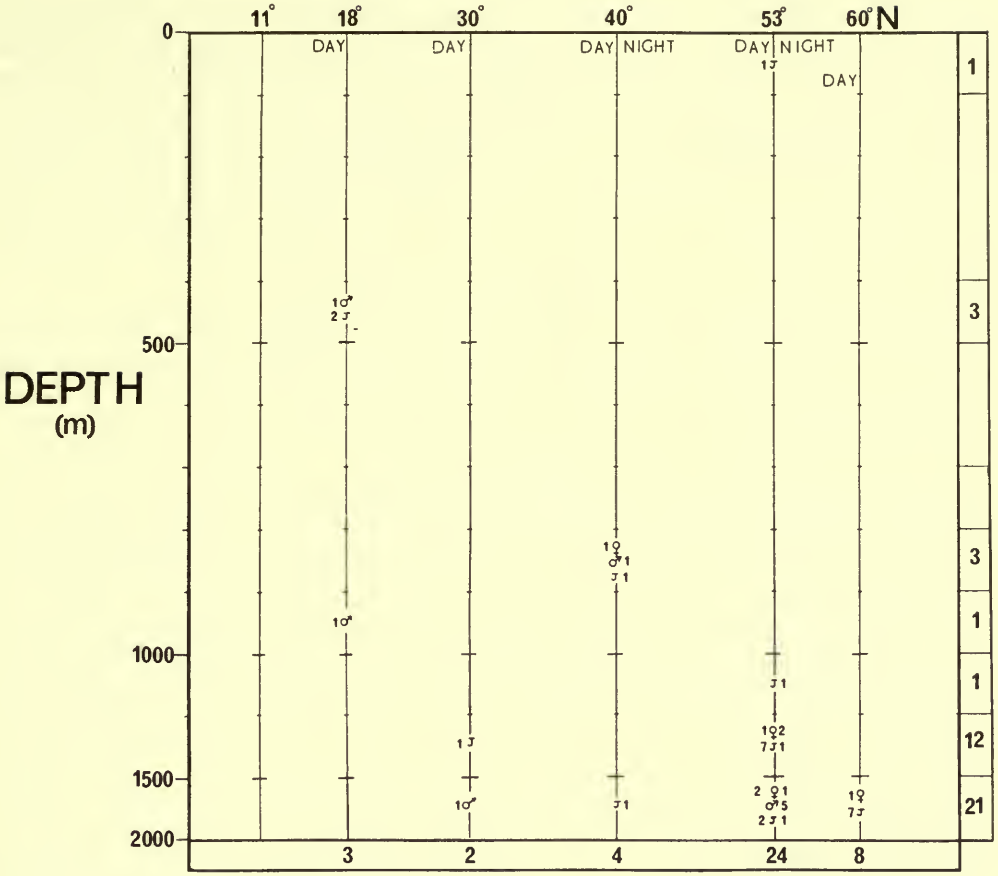

FIG. 22. *Conchoecia gaussi*. Depth distribution of various latitudes in the Northeast Atlantic Ocean. For explanation see Fig. 19.

It is notable that most species of *Conchoecia* occurring in the Arctic have Antarctic counterparts (*C. borealis* Sars, 1866, *C. antipoda* Müller, 1906, *C. obtusata* Sars, 1866, *C. elegans* Sars, 1866). Only *C. maxima* Brady & Norman, 1896 is endemic to the Arctic region although this species is closely related to *C. borealis*/*C. antipoda*. On the other hand, several species appear to be endemic to the Antarctic area (*C. belgica* Müller, 1906, *C. chuni* Müller, 1906, *C. hettacra* Müller, 1906, *C. isocheira* Müller, 1906, *C. schwabenlandica* Hartmann, 1962, *C. serrulata* Claus, 1874). Should *C.* aff. *edentata* prove to be conspecific with Müller's *C. edentata*, then this will be another species having a bipolar distribution.

C. subedentata sp. n. and *C.* aff. *edentata* are to some extent sympatric and this raises the question of how competition between these two closely related species is reduced far enough to allow their coexistence. The mandibular structure is virtually identical in both species and so they presumably eat the same sort of food. The main factor may thus be the larger body size of *C.* aff. *edentata* allowing it to eat larger food particles than *C. subedentata* sp. n. (Angel pers. comm.). This may also apply to juvenile instars since the lengths of the few measured *C.* aff. *edentata* juveniles tend to fall between the peaks on the length histogram for adult and juvenile stages of *C. subedentata* sp. n. (Fig. 1); however, more measurements are needed to confirm this pattern. A similar situation is well known in calanoid copepods where the coexistence of closely related sympatric species has been attributed in part to size differences (for example, Sandercock, 1967; Hutchinson, 1967 : 680–684; Hammer & Sawchyn, 1968). Competition must also be reduced by the partial depth separation of the two species (Figs 19, 20).

There is a different pattern of size distribution in the *gaussi* group. Here, adults and juveniles of *C. gaussi* and *C. incisa* do not interdigitate but fall into three or four fairly distinct size classes (Fig. 10); (i) Stage V juveniles of *C. incisa*; (ii) adult males and Stage VI juveniles of *C. incisa* and Stage V instars of *C. gaussi*; (iii) adult females of *C. incisa* and Stage VI juveniles of *C. gaussi*; (iv) adult males and females of *C. gaussi* may be regarded as forming a fourth group although the size range here is greater and the group poorly defined. As in the *edentata* group, competition between the size groups is probably reduced by the difference in size of the food particles that members of each group are able to eat. However, groups (ii) and (iii) include both juveniles of *C. gaussi* and adults and juveniles of *C. incisa* and since these species coexist to some extent (Figs 21, 22) some factor other than size must reduce competition between them. In *C. incisa* the cutting edge of the mandibular coxale is straight while in *C. gaussi* it is toothed, hence a difference in diet reflected by the dissimilar mandibular structure seems the most likely way that competition is minimized. Again an analogy may be drawn with freshwater calanoid copepods where Maly & Maly (1974) found that two closely related sympatric species with different mandibular structure had dissimilar diets.

From the above discussion three possible methods of avoiding or reducing competition between closely related sympatric species of *Conchoecia* may be suggested. (i) Depth separation, as is partially the case with *C. subedentata* sp. n. and *C.* aff. *edentata*. (ii) Differences in the size of food particle eaten as reflected by differences in body size; here one would expect the adult and juvenile size ranges of closely related species to interdigitate as apparently happens in the *edentata* group. (iii) Differences in diet reflected by dissimilar mandibular structure; this would allow closely related species of similar size to coexist as with adults and juveniles of *C. incisa* and juveniles of *C. gaussi*.

ADDENDUM

After this paper was submitted, Dr G. B. Deevey kindly sent me two females of *C. edentata* from Stations 18 and 25 of the Hudson 70 Expedition (Deevey 1974). The specimens are mounted on slides and before dissection measured 1·70 mm and 1·77 mm long. The relative lengths of the setae on the final segment of the sixth limb and the single seta near the spine teeth on the mandibular basale suggest that Deevey's specimens are probably my *C.* aff. *edentata*. Dr Deevey also sent me some material identified as *C. edentata* from Station S off Bermuda. It comprises some undissected specimens in formalin and four mounted males and females which were collected in 1969 and 1970 and so not included in Deevey's (1968) paper. These specimens clearly belong to *C. subedentata* and the occurrence of this species near Bermuda is confirmed by its presence at *Discovery* station 8281.

Dr Angel has restudied Fowler's (1909) material in the British Museum (Natural History). He reports (pers. comm.) that Fowler's (1909 : 255, pl. 25, figs 258–262) female specimen of *Conchoecia* C belongs in *C. subedentata* sp. n.

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ZOOLOGY Vol. 30 No. 4
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Marine Biological Association of the U.K.
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British Museum (Natural History)

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ECHINODERMS FROM THE NORTHERN REGION OF THE GREAT BARRIER REEF, AUSTRALIA

By P. E. GIBBS, AILSA M. CLARK & CHRISTINE M. CLARK

SYNOPSIS

This paper gives records of about 140 species of echinoderms from the northern region of the Great Barrier Reef collected during the Royal Society–Universities of Queensland Expedition in 1973. One ophiuroid species is new to science, namely *Amphiura phrixocantha* sp. nov. (p. 121). Ten other ophiuroids, two echinoids and one holothurian are new to the Australian fauna and the ranges of eight more ophiuroids and one holothurian are extended to the Great Barrier Reef Province from other parts of Australia. In addition, a few unpublished records from relevant material in the British Museum collections are included and notes are given on several species of especial interest. In contrast to most shallow-water tropical collections, the one from this Expedition includes a high proportion of burrowing species from soft substrates. A list of some animal associates of the specimens collected is appended.

INTRODUCTION

EARLY investigations of the echinoderm fauna of the Great Barrier Reef were largely centred on the Torres Strait region and essentially began with the visit of the *Challenger* Expedition in 1874. The material collected, mostly from dredging, together with that taken by the *Alert* Expedition in 1881, provided records for a basic list of about 80 species. Subsequently, two land-based expeditions, firstly that of R. Semon in 1892 and later that of the Carnegie Institution of Washington in 1913, increased the number of species known in the area to about 250 (H. L. Clark, 1915, 1921).

South of Torres Strait along the east coast of Queensland early records of echinoderms were provided by the observations and collections of Tenison-Woods (1880a, b) made in the Port Douglas–Trinity Bay area and by the *Alert* Expedition, collecting particularly from Port Curtis, Port Molle and Port Denison (see Bell, 1884). The next substantial collection was not made until 1924 when W. E. J. Paradice took about 60 species, chiefly between the latitudes of 17° and 19°S (H. L. Clark, 1926; McNeill & Livingstone, 1926). This collection also included specimens from Low Isles (16°23′S), the echinoderm fauna of which is now well known as a result of the surveys by the Great Barrier Reef Expedition in 1928–29 (H. L. Clark, 1932; Livingstone, 1932) and the Great Barrier Reef Committee in 1954 (Endean, 1956). In recent years, further echinoderm records (excluding crinoids) have been compiled by Endean (1953, 1961, 1965), while crinoids from the Swain Reefs Expedition of 1962 have been dealt with by A. M. Clark (1975).

The Great Barrier Reef as a zoogeographical region has been discussed in detail by such authors as Whitley (1932), H. L. Clark (1946) and Endean, Kenny & Stephenson (1956). In the present paper, the Great Barrier Reef Province is taken to include the sea area east of longitude 142°E (just west of Torres Strait) down to a depth of 200 m, from Anchor and Bramble Cays (between 9°00′S and 9°20′S) in the north to Fraser Island including Hervey Bay (effectively the latitude of 25°S) in the south. Echinoderm records from the Queensland coast are summarized by H. L. Clark (1946) and, except for crinoids, by Endean (1957) with later additions also by Endean (1961, 1965). Within the geographical limits defined above it appears that about 310 species of echinoderms have been recorded from shallow-water ; however, many of these species are known from relatively few localities and/or specimens and records are particularly sparse for the northern part of the Great Barrier Reef outside the Torres Strait region. Accordingly a list of the echinoderms collected in this area during the 1973 expedition should be of some zoogeographic value, especially as very little systematic dredging or trawling has previously been undertaken in the region as a whole (Dall & Stephenson, 1953).

The echinoderm records given in the present paper result from the material collected during the Royal Society–Universities of Queensland Expedition to the Great Barrier Reef which took place from July to November 1973. The investigations of Phases I and II of the Expedition were mostly concerned with the structure and ecology of islands and reefs between Cairns and Pipon Island (approximately 17°S to 14°S) but Phase III operations extended northwards to Raine Island (11°36′S).

Most of the records given below, particularly those of ophiuroids, originate from a benthic survey carried out using naturalist and anchor dredges (Forster, 1953) and involving bottom sampling at 62 stations in depths of 4–64 m between the latitudes of 16°42′S to 11°40′S. Station data are given in Table 1.

TABLE 1

The positions of the stations at which dredge samples were taken in the northern part of the Great Barrier Reef, with depth, description of deposit and date of collection also given

STATION	LATITUDE (S)	LONGITUDE (E)	DEPTH (m)	DEPOSIT	DATE (1973)
D1	14°25·2′	144°47·9′	15	Muddy sand with many forams	5 Aug.
D2	14°25·1′	144°48·6′	15	Muddy sand with many forams	5 Aug.
D3	14°24·9′	144°50·1′	16	Muddy sand with many forams	6 Aug.
D4	14°27·1′	144°53·8′	20	Muddy sand with many forams	6 Aug.
D5	14°28·7′	144°55·7′	18	Muddy sand with many forams	6 Aug.
D6	14°29·2′	144°57·8′	26	Muddy sand with many forams	6 Aug.
D7	14°28·8′	145°0·2′	26	Muddy sand with many forams	7 Aug.
D8	14°28·0′	145°0·0′	26	Muddy sand with many forams	7 Aug.
D9	14°26·7′	144°58·9′	37	Shell gravel	7 Aug.
D10	14°29·2′	144°57·1′	20	Shell gravel	7 Aug.
D11	14°21·1′	144°53·6′	22	Muddy sand with many forams	8 Aug.
D12	14°17·9′	144°53·4′	24	Muddy sand with shells	8 Aug.
D13	14°14·8′	144°53·2′	22	Shell gravel	8 Aug.
D14	14°15·8′	144°51·1′	33	Muddy fine sand with shells	8 Aug.
D15	14°22·6′	144°50·2′	16	Muddy sand with forams	8 Aug.
D16	14°32·2′	144°53·4′	11	Muddy sand with shells	9 Aug.
D17	14°34·2′	144°52·2′	4	Clean medium sand with shells	9 Aug.

Table 1 (cont.)

Station	Latitude (S)	Longitude (E)	Depth (m)	Deposit	Date (1973)
D18	14°34·0′	144°50·5′	4	Clean coarse sand with calcareous algae	9 Aug.
D19	14°31·8′	144°50·7′	9	Muddy sand with shells	9 Aug.
D20	16°40·4′	145°57·8′	22	Silty mud with many forams	16 Aug.
D21	16°40·4′	145°59·1′	24	Silty mud with many forams	16 Aug.
D22	16°40·3′	146°0·2′	27	Calcareous mud with few forams	16 Aug.
D23	16°39·2′	146°1·2′	27	Muddy sand with many forams	17 Aug.
D24	16°40·1′	146°1·2′	29	Calcareous mud with many bivalves	17 Aug.
D25	16°40·7′	146°1·0′	27	Calcareous mud with many bivalves	17 Aug.
D26	16°41·1′	146°0·8′	22	Muddy sand with many forams	17 Aug.
D27	16°38·1′	145°57·8′	27	Silty mud with many forams	18 Aug.
D28	16°39·2′	145°57·6′	27	Silty mud with many forams	18 Aug.
D29	16°41·6′	145°57·3′	9	Clean medium sand	18 Aug.
D30	15°44·3′	145°27·8′	11	Muddy fine sand	31 Aug.
D31	15°44·3′	145°27·7′	11	Muddy fine sand	31 Aug.
D32	15°44·0′	145°27·1′	18	Muddy fine sand with forams	31 Aug.
D33	15°43·2′	145°27·4′	16	Sandy silt – few forams	31 Aug.
D34	15°43·8′	145°29·2′	27	Mud with coral fragments	1 Sept.
D35	15°44·4′	145°31·1′	27	Mud	1 Sept.
D36	15°45·0′	145°33·0′	37	Mud with coral and shell	1 Sept.
D37	15°45·6′	145°35·0′	29	Calcareous mud	1 Sept.
D38	15°42·9′	145°25·6′	21	Muddy coarse sand with forams	2 Sept.
D39	15°40·9′	145°22·9′	20	Muddy sand with many shells	2 Sept.
D40	15°39·3′	145°22·0′	18	Muddy sand with much shell	2 Sept.
D41	15°37·8′	145°21·0′	16	Muddy sand with shells	2 Sept.
D42	15°39·5′	145°29·4′	16	Calcareous mud with coral	4 Sept.
D43	15°39·0′	145°28·8′	18	Calcareous mud with coral	4 Sept.
D44	15°38·3′	145°28·0′	16	Coral blocks	4 Sept.
D45	15°37·3′	145°26·5′	22	Muddy sand with many forams	4 Sept.
D46	14°44·0′	145°11·6′	9	Muddy sand with few forams	1 Oct.
D47	14°43·7′	145°12·1′	9	Muddy sand with few forams	1 Oct.
D48	14°43·4′	145°11·0′	7	Muddy sand with few forams	1 Oct.
D49	14°42·6′	145°10·1′	7	Muddy sand with few forams	1 Oct.
D50	14°36·8′	145°28·7′	22	*Halimeda* sand	21 Oct.
D51	14°37·2′	145°26·3′	22	Silty sand with forams	21 Oct.
D52	14°39·3′	145°25·7′	24	Silty sand with forams	21 Oct.
K1(A)	13°28·2′	143°42·0′	22	Sticky black mud	28 Oct.
K2(A)	13°12·2′	143°34·1′	11	Sticky black mud	29 Oct.
K3(A)	11°50·0′	143°34·2′	64	Silty fine sand with shells	31 Oct.
K3(N)	,,	,,	,,	,,	5 Nov.
K4(A)	11°40·4′	143°57·8′	35	*Halimeda* sand	3 Nov.
K5(A)	11°40·4′	143°58·5′	34	Silty sand with *Halimeda*	3 Nov.
K6(A)	11°40·4′	143°59·3′	36	*Halimeda* sand	3 Nov.
K7(N)	11°40·2′	144°0·2′	22	Medium-coarse sand	3 Nov.
K8(N)	11°48·4′	143°21·4′	18	Silty sand with forams	6 Nov.
K9(N)	12°9·0′	143°13.2′	24	Black mud with shells	7 Nov.
K10(N)	12°18·0′	143°19·6′	34	Black mud with shells	8 Nov.

Stations D1–D52 were sampled with a naturalist dredge, Stations K1–K10 with anchor (A) and/or naturalist (N) dredge.

Table 2

Positions of islands and reefs where collections of littoral echinoderms were made. Dates of collection and survey station numbers are given

Locality	Latitude (S)	Longitude (E)	Date	Survey stations
Beesley	12°14·5′	143°12·0′	7 Nov.	
Bewick	14°26·0′	144°48·6′	9 Aug.	
Bird	11°45·4′	143°05·2′	6 Nov	
Hampton	14°33·8′	144°53·2′	11 Aug	
Howick	14°30·2′	144°58·4′	8 Aug	
Ingram	14°30·0′	144°52·8′	22/23 Oct	IN.1–IN.3 Z4–Z5
Lark Passage (reef to N of)	15°06·0′	145°44·0′	25 Sept	
Lizard	14°40·0′	145°28·0′	21 Oct	LD/Z3
Low	16°23·2′	145°34·0′	23/30 Aug	L1–L7
Mid Reef	14°27·5′	144°57·5′	10 Aug	
Noble	14°30·4′	144°46·0′	23 Oct	
Pelican	13°55·0′	143°50·0′	29 Oct	
Pipon	14°07·4′	144°31·5′	25 Oct	
Three	15°07·0′	145°25·5′	6/28 Sept	3.1–3.11 Z1–Z2
Turtle I	14°44·0′	145°11·3′	29 Sept/14 Oct	TIA–TIC
Turtle IV	14°43·2′	145°12·2′	8 Oct	
Two	15°01·3′	145°26·6′	20/22 Sept	2·1–2·4
Watson	14°28·0′	144°53·5′	28 July	

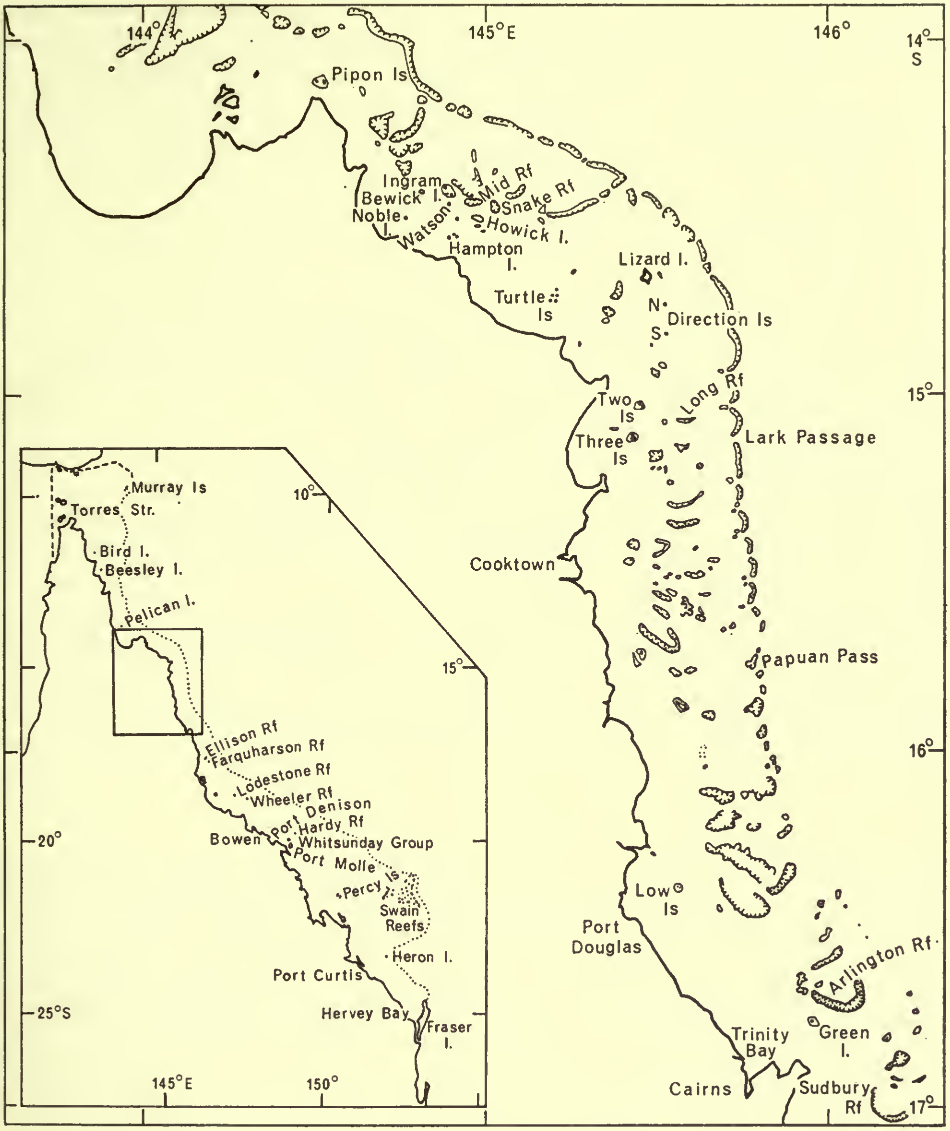
Table 3

British Museum echinoderm collection : additional unpublished localities

Locality (Reef)	Latitude (S)	Longitude (E)	Depth (m)
Farquharson	17°47·5′	146°31·0′	3–6
Lodestone	18°41·5′	147°06·0′	
Sudbury	17°00·0′	146°13·0′	3–6
Wheeler	18°48·5′	147°31·5′	

Littoral investigations were chiefly directed towards a survey of the fauna inhabiting the intertidal sand and mud flats on those islands and reefs visited by the Expedition. Stations are prefixed by the initial letter(s) of the island name (Table 2) : details of this survey will be published elsewhere (Gibbs, 1976). In addition, collections of echinoderms were also made on reef flats ; for the most part these species were living either under coral boulders or in crevices. Sublittoral crinoids were kindly sampled by Mr L. Zell at five localities (designated Z stations), all at 3–5 m depth, as follows :

Z1 – Three Isles – north end, off sand cay, September 23.
Z2 – Three Isles – south-east, off mangrove island, September 26.
Z3 – Lizard Island – off north-east promontory, October 21.
Z4 – Ingram Island – south-west of sand cay, October 22.
Z5 – Ingram Island – north-west of sand cay, October 23.


144°
145°E
146°
14° S
Pipon Is
Ingram
Bewick I.
Noble
Watson
Mid Rf
Snake Rf
Howick I.
Hampton I.
Lizard I.
Turtle Is
N.
S.
Direction Is
Long Rf
15°
Two Is
Three Is
Lark Passage
Cooktown
Papuan Pass
16°
Low Is
Port Douglas
Arlington Rf
Trinity Bay
Green I.
Cairns
Sudbury Rf
17°
Murray Is
Torres Str.
10°
Bird I.
Beesley I.
Pelican I.
15°
Ellison Rf
Farquharson Rf
Lodestone Rf
Wheeler Rf
Port Denison
Hardy Rf
Bowen
Whitsunday Group
Port Molle
Percy Is
Swain Reefs
Heron I.
Port Curtis
20°
25°S
Hervey Bay
Fraser I.
145°E
150°

Map showing collecting localities

The Expedition collection is composed of about 450 specimens consisting of about 140 species plus about 12 samples of immature or incomplete specimens not positively identifiable to species. About two-thirds of the species are represented by only one or two specimens but this need not imply rarity in many cases since the larger littoral forms for example, particularly the species of holothurians, were purposely collected only once or twice, although generally common and widespread. The class Crinoidea is represented by 15 species, Asteroidea by 17, Ophiuroidea by 56, Echinoidea by 21 and Holothurioidea by 29 species. Of these totals it would appear that 11 ophiuroids (including 1 new species), 2 echinoids and 2 holothurians* are recorded for the first time from Australian waters and 8 further ophiuroids and 1 holothurian newly from the Great Barrier Reef Province. These species are indicated in the systematic account. Twenty-two of the species are not listed by A. M. Clark & Rowe (1971) as occurring in some part of the whole of northern Australia, so that the number of species from this area is increased to about 460 ; the total number of species for the Great Barrier Reef Province rises to about 330.

Considerable faunistic information is available for Low Isles as a result of the surveys of 1928–29 and 1954. The 1973 expedition spent just seven days at Low Isles but it is worth noting that seven species of echinoderms, previously unrecorded for these islands, were taken. These are *Gomophia egyptiaca*, *Amphioplus* (*Lymanella*) *bocki*, *Amphiura diacritica*, *Schizaster lacunosus*, *Leptosynapta latipatina*, *Opheodesoma grisea* and *Chiridota rigida*.

The bulk of the echinoderm material collected on the Royal Society–Universities of Queensland Expedition has been deposited in the collections of the British Museum (Natural History). Selected specimens donated to the Australian Museum, Sydney, are indicated in the text by the numbers in square brackets [ ]. The paratype of *Amphiura phrixocantha* sp. nov. only, is in the Queensland Museum.

This report was initiated by one of us (P. E. G.) who drew up the introduction, list of associated animals (see Table 4, p. 141) and record data for the species using identifications made by the others. The notes on individual species of crinoids are by A. M. C., those on echinoids and holothurians by C. M. C., the two combining on ophiuroids so that the new species is the responsibility of both Clarks.

SPECIES COLLECTED

For each species the locality or station and number of specimens are given, details being found in Tables 1 and 2. Sight records of distinctive species (not collected) are indicated by 'S'. In the case of those species for which few locality or specimen records from the Great Barrier Reef Province exist, these are cited together with any unpublished records from the British Museum collections (Table 3). The remaining species are considered to be widespread in the Province (see Endean, 1957) and a blanket distribution for them can be assumed. References are kept to a minimum by citing, wherever possible, H. L. Clark (1946), or an alternative reference from which the original description can be traced. Synonyms and other combinations used by H. L. Clark, Livingstone and Endean are included.

Class *CRINOIDEA*

COMASTERIDAE

Capillaster multiradiatus (Linnaeus, 1758)

See : H. L. Clark, 1946 : 27.
D52 – 1 ; K3 – 1.

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* One of these is the species here named '*Rynkatorpa* sp. nov.'. Since this paper went to press Dr Rowe has provided a specific name and description, to be published shortly in this Bulletin.

Comantheria briareus (Bell, 1882)

See : H. L. Clark, 1946 : 34.
Three Is (Z2) – 4[1].
Previous records : Port Denison ; Outer Reef between 17°S and 19°S (H. L. Clark, 1946).

Comantheria or ***Comanthus*** sp.

D51 – 1.

This specimen is immature with only 18 very slender arms, *c.* 70 mm long, and few division series – hence the uncertainty as to genus. Three arms arise direct from the first (IBr) division series. The proximal ossicles are smooth. The centrodorsal is very reduced, in the form of a flat pentagon marked by subradial clefts. It bears a single cirrus socket and four small 'buds' of cirri. One IIIBr series is present ; this has four ossicles (like all seven IIBr series) and is an outer one. On this account the specimen is more like *Comanthus parvicirrus timorensis* than *Comantheria briareus*, which usually has only two ossicles in the IIIBr series.

Comanthina schlegeli (P. H. Carpenter, 1881)

See : H. L. Clark, 1946 : 33.
Three Is (Z2) – 1 ; Lizard I. (Z3) – 1.
Previous records : Murray Is (3 specimens) ; Percy Is (1 specimen), (H. L. Clark, 1946).

Comanthus bennetti (J. Müller, 1841)

See : H. L. Clark, 1946 : 36 (as *Cenolia bennetti*) ; A. M. Clark & Rowe, 1971 : 16 (as *Comanthus bennetti*).
Lizard I. (Z3) – 1.
B.M. collections : Wheeler Reef, near Townsville (3 specimens).
Previous records : Port Denison ; north of N Direction I. (2 specimens) (H. L. Clark, 1946).

Comanthus parvicirrus (J. Müller, 1841)

See : H. L. Clark, 1946 : 39 ; A. M. Clark, 1975 : 395.

SYNONYMS : *Comanthus annulata* (Bell, 1882) H. L. Clark, 1921 ; *Comanthus callipepla* H. L. Clark, 1915 ; *Comanthus timorensis* (J. Müller, 1841) H. L. Clark, 1946.

Howick I. (north side at 3 metres depth) – [1] ; Three Is (Z1) – 2 ; Ingram I. (Z5) – 2 ; Lark Passage (reef flat) – 2.

Comanthus samoanus A. H. Clark, 1909

See : H. L. Clark, 1946 : 36 (as *Cenolia samoana*) ; A. M. Clark & Rowe, 1971 : 16 (as *Comanthus samoanus*).
Ingram I. (Z4) – 1 ; (Z5) – 2 ; Lark Passage (reef flat) – 1.

Comatella nigra (P. H. Carpenter, 1888)

See : H. L. Clark, 1946 : 25 ; A. M. Clark, 1975 : 392.
D52 – 1.
B.M. collections : Wheeler Reef, near Townsville (2 specimens).
Previous records : Murray Is ; Lizard I. (H. L. Clark, 1946) ; Swain Reefs (A. M. Clark, 1975).

This specimen does not help to solve the problem of the distinction between *Comatella nigra* and *Comatella stelligera* mentioned by A. M. Clark (1975). It has only 28 arms, so running down to *C. stelligera*, but the arm length is only *c.* 55 mm so the infrequency of them could be accountable to immaturity. One of the few mature cirri remaining has as many as 26 segments, the division series are well separated laterally and smooth and the arms feel smooth when stroked distalwards, since only fine grooving develops on the middle and distal brachials, all characters justifying its identification as *C. nigra*.

However, seven specimens of *Comatella* from the Easter Group, Abrolhos Islands, Western Australia (collected by a recent Aquinas College expedition) do fall easily into two distinct groups. Three of them have *c.* 54, 59 and *c.* 60 arms, smooth to the touch, and up to *c.* 31, 31 (or ? 32) and 35 cirrus segments (cirrals) – agreeing with *C. nigra* – as opposed to 28, 29, 29 and 29 arms, rough in texture, and up to only 21, 22, 23 and 23 cirrals respectively in the remaining four specimens, which are referable to *C. stelligera*. The arm length is 75–90 mm in the former (*nigra*) and 90–110 mm in the latter, giving no significant size difference.

The cirri are remarkably reduced in this Queensland specimen, only VII mature ones remaining besides about ix more or less reduced immature ones and about six obsolete cirrus sockets. The number is usually XX–XXX.

Comatella stelligera (P. H. Carpenter, 1880)

See : H. L. Clark, 1946 : 26.
Three Is. (Z1) – 1.

This specimen has 29 fairly crowded arms, with little space between the division series laterally and up to only 23 cirrus segments, agreeing with *C. stelligera*.

Comatula pectinata (Linnaeus, 1758)

See : H. L. Clark, 1946 : 31 ; A. M. Clark, 1975 : 394.
K3 – 1.

Comatula purpurea (J. Müller, 1843)

See: A. M. Clark, 1975 : 394.
D8 – 1.

Comatula rotalaria Lamarck, 1816

See: H. L. Clark, 1946 : 29 (as *Validia rotalaria*); A. M. Clark, 1975 : 393 (as *Comatula* (*Validia*) *rotalaria*).
D7 – 1.

HIMEROMETRIDAE

Himerometra robustipinna (P. H. Carpenter, 1881)

See: H. L. Clark, 1946 : 42.
Bewick I. (7 m depth) – 2; Three Is (Z2) – 1; Lizard I. (Z3) – 3.
B.M. collections: Farquharson Reef (4 specimens); Sudbury Reef (1 specimen).
Previous records: Ellison Reef (2 specimens) (H. L. Clark, 1946).

One of the three specimens from Lizard Island is aberrant in three characters. Firstly, its enlarged basal pinnules are almost smooth in profile, the segments not being individually flared at their distal ends, while they number from 26 to as many as 32 on the few that are still intact. In *H. robustipinna* the maximum number given by A. H. Clark is 24 segments. Secondly, of the up to 39 segments of the peripheral cirri, as many as 20 of the distal ones have a fairly well-developed blunt, nose-like dorsal spine. In *H. robustipinna* usually less than ten distal segments are described as having a small median tubercle and sometimes this may be negligible. Thirdly, the middle brachials are more markedly flared and more rugose at their distal ends than in the remaining specimens, though A. H. Clark and others appear to give little weight to this character, which is hardly mentioned in the published descriptions of the species of *Himerometra*.

This aberrant specimen seems to approximate to *Himerometra bartschi* A. H. Clark, 1908, known from Singapore to the Kei Islands, in the relatively large number of segments in the proximal pinnules (though as many as 40 are described for *H. bartschi*) which are also fairly smooth, and in the greater development of dorsal spines on the distal cirrus segments (about 25 segments being spinose in *H. bartschi*, described as 'small but prominent'). However, A. H. Clark considers *H. robustipinna* to be a particularly variable species and in the holotype itself the proximal pinnules are relatively smooth. The difference in the cirri may be more significant but better sampling is needed to show whether or not a second species of *Himerometra* can be recognized from Australian waters.*

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* Since completion of this paper, another specimen from Lizard Island (North Reef, 18 m, collected by Neville Coleman) has come to hand. This too has relatively smooth basal pinnules, stout basally but slender and flagellate terminally, P_D having up to 27 segments. Two intact mature cirri with 31 and 34 segments have dorsal spines from about the twelfth. Both these characters agree with the aberrant specimen but the brachials, though becoming slightly flared, are not rugose.

COLOBOMETRIDAE

Colobometra perspinosa (P. H. Carpenter, 1881)

See : H. L. Clark, 1946 : 52.
Lizard I. (Z3) – 1.

Oligometra carpenteri (Bell, 1884)

See : H. L. Clark, 1946 : 49.
D21 – 1.

TROPIOMETRIDAE

Tropiometra afra (Hartlaub, 1890)

See : H. L. Clark, 1946 : 53.
Ingram I. (Z4) – 6 ; (Z5) – 1.
B.M. collections : Lodestone Reef, NE of Townsville (1 specimen) ; Wheeler Reef, near Townsville (2 specimens).
Previous records : Murray Is (3 specimens) ; Bowen (2 specimens) (H. L. Clark, 1946).

Subclass *ASTEROIDEA*

ASTROPECTINIDAE

Astropecten granulatus Müller & Troschel, 1842

See : H. L. Clark, 1946 : 76.
K9 – 1.

ARCHASTERIDAE

Archaster typicus Müller & Troschel, 1840

See : H. L. Clark, 1946 : 79.
Hampton I. (reef flat) – 3[2] ; Low Is (L4) – 3 ; Three Is (L5) – S.

GONIASTERIDAE

Stellaster equestris (Retzius, 1805)

See : H. L. Clark, 1946 : 97 (as *Stellaster incei*) ; A. M. Clark & Rowe, 1971 : 49 (as *Stellaster equestris*).
D19 – 1.

Stellaster sp. juv. aff. ***S. equestris*** (Retzius)

K6 – 1 ; K9 – 1.

OREASTERIDAE

Culcita novaeguineae Müller & Troschel, 1842

See : H. L. Clark, 1946 : 108.
Low Is. – S ; Three Is – S.

Pentaceraster regulus (Müller & Troschel, 1842)

See : H. L. Clark, 1946 : 107 (as *P. australis*) ; Endean, 1953 : 54 (as *P. australis*) ; A. M. Clark & Rowe, 1971 : 55 (as *P. regulus*).
D17 – 2 ; D18 – 1.

Protoreaster nodosus (Linnaeus, 1758)

See : H. L. Clark, 1946 : 106.
D18 – 4.

OPHIDIASTERIDAE

Fromia sp. juv.

Lizard I. (Z3) – 1 (on crinoid *Comanthus bennetti*).

Gomophia egyptiaca Gray, 1840

See : Endean, 1965 : 230.
Low Is (off NE shore at 3 m depth) – 1.
Previous record : Heron I. (2 specimens), (Endean, 1965).

Linckia laevigata (Linnaeus, 1758)

See : H. L. Clark, 1946 : 117.
Mid Reef – S ; Three Is – S ; Lark Passage – S.

Nardoa mamillifera Livingstone, 1930

See : H. L. Clark, 1946 : 116.
D44 – 1.
Previous record : Murray Is (Livingstone, 1930).

Nardoa pauciforis (von Martens, 1866)

See : H. L. Clark, 1946 : 115.
Mid Reef – S ; Three Is – S.

Ophidiaster granifer Lütken, 1872

See : H. L. Clark, 1946 : 121.
Turtle IV I. (reef flat) – 2.

METRODIRIDAE

Metrodira subulata Gray, 1840

D48 – 1 (juvenile identified by Mrs Loisette M. Marsh).

ASTEROPSEIDAE

Asteropsis carinifera (Lamarck, 1816)

See : H. L. Clark, 1946 : 109 (as *Asterope carinifera*) ; Endean, 1956 : 124 (as *Asterope carinifera*) ; A. M. Clark & Rowe, 1971 : 65 (as *Asteropsis carinifera*).
Low Is (*Tripneustes* spit) – 1 ; Lark Passage (reef flat) – 1.

ASTERINIDAE

Nepanthia brevis (Perrier, 1875)

See : H. L. Clark, 1946 : 141.
North of Snake Reef at 14°26·2′S : 145°0·7′E (Grab st. 115), 24 m depth, mud – 1.

Patiriella pseudoexigua Dartnall, 1971

See : H. L. Clark, 1946 : 136 (as *Patiriella exigua* [part]) ; Endean, 1953 : 54 (as *Patiriella exigua*) ; 1956 : 125 (as *Patiriella exigua*) ; Dartnall, 1971 : 43 (as *Patiriella pseudoexigua*). [Non *Asterias exigua* Lamarck, 1816.]
Three Is (3.7) – [1] ; Turtle I I. (TIC) – 3.

ACANTHASTERIDAE

Acanthaster planci (Linnaeus, 1758)

See : H. L. Clark, 1946 : 150.
Ingram I. (Z4, Z5) – S.

Subclass *OPHIUROIDEA*

EURYALIDAE

Euryale aspera Lamarck, 1816

See : H. L. Clark, 1946 : 172.
K3 – 2.

OPHIOMYXIDAE

Ophiomyxa australis Lütken, 1869

See : H. L. Clark, 1946 : 170.
K6 – 1.

OPHIACANTHIDAE

Ophiacantha ?confusa Koehler, 1905

See : H. L. Clark, 1946 : 184.
K3 – 1.

AMPHIURIDAE

The disc of many burrowing amphiurids is very vulnerable to loss during collection and accordingly several of these specimens cannot be determined as to species.

Amphiodia sp. juv.

D2 – 1 ; D21 – 2.

Amphioplus (Amphioplus) didymus H. L. Clark, 1938 (Fig. 1a)

See : H. L. Clark, 1946 : 206 ; A. M. Clark & Rowe, 1971 : 101, fig. 48d, e.
D1 – 1 ; D3 – 1 ; D15 – 1(no disc).

These specimens provide a new record for the Great Barrier Reef Province. The holotype was taken at Broome, NW Australia, and a paratype at Darwin, the type-locality of the very similar *Amphioplus stenaspis* H. L. Clark. H. L. Clark's descriptions and figures of these two species (1938) indicate that they can be distinguished by the contiguity of the radial and adoral shields and the arrangement of the oral papillae. However, his description contradicts his figure of *A. didymus* with regard to the adoral shields, which are in fact broadly contiguous in the holotype, as in *A. stenaspis*, while the present material from Queensland indicates that the radial shields may also be contiguous distally in *A. stenaspis*. (Incidentally the second point throws further doubt on the validity of *Amphioplus iuxtus* Murakami, 1943 from the Caroline Islands as distinct from *A. stenaspis*, commented on by A. M. Clark in 1971.) The character of the arrangement of the oral papillae in a concave row (in *A. didymus*) as opposed to a straight line concealing more of the oral tentacle scale (in *A. stenaspis*) used in the 1971 key to distinguish the two, is also now found to be variable. This leaves only the distinctive bihamulate shape of the second from lowest arm spine beyond the arm base in *A. didymus* as a reliable diagnostic character ; this spine in *A. stenaspis* is simply blunt distally (Fig. 1b).

Amphioplus didymus is also liable to be confused with *Amphioplus* (*Lymanella*) *bocki* Koehler (see below) which similarly has two very large tentacle scales and the second arm spine modified – though in the case of *A. bocki* no more than broad spatulate in the Queensland specimens. The most obvious distinctions are that *A. bocki* has only three arm spines proximally, the arms themselves are relatively longer (about 12 times the disc diameter), the radial shields are relatively broader and more fully contiguous and the dorsal arm plates are elliptical rather than blunted rectangular in shape.

Amphioplus (Amphioplus) impressus (Ljungman, 1867)

See : A. M. Clark, 1970 : 63, fig. 9l, m.
D22 – 2 ; D36 – 1 ; D40 – [1].

This is a new record for Australian waters. The species was previously known from various localities in the East Indies, including Timor and New Guinea approximating to Australia, from the Philippines and from Marovo lagoon, Solomon Islands, collected by Gibbs in 1965 (unpublished).

Amphioplus impressus may be confused with the following species, *Amphioplus intermedius*, since both are unusual among species of *Amphioplus* s.s. in having the distalmost oral papilla markedly broadened. Also the disc is fully scaled, often with a sharp edge, the radial shields are more or less fully contiguous, the arm spines number three and the two tentacle scales are moderate in size. The most obvious difference is that *A. impressus* has coarser, very well-defined disc scales (a minimum of six across the shortest line between two radial shields interradially in a specimen with d.d. 4·5 mm compared with *c.* 10 in *A. intermedius* with d.d. 2·5 mm). The rosette is also conspicuous in specimens of *impressus* with original (as opposed to regenerated) discs, the dorsal arm plates of that species also have a median distal angle and the first ventral arm plate is completely superficial, fitting up against the distal edges of the two outermost oral papillae rather than being overlain by them proximally.

Amphioplus (Amphioplus) intermedius (Koehler, 1905)

See : A. M. Clark, 1970 : 45, 64.
D2 – 1.

This too is a new record for Australian waters. The species was previously known from the East Indies off Java and the Borneo Bank. Comparative remarks with *A. impressus* are given above.

Amphioplus sp. aff. **A. intermedius** (Koehler)

D39 – 2(no discs).

Amphioplus (Amphioplus) lucidus Koehler, 1922

See : H. L. Clark, 1946 : 204.
D8 – 1 ; D41 – 1 ; K3 – 1.

A new record for the Great Barrier Reef Province. The species was previously known to the west from Broome, NW Australia, and to the south-east from Broken Bay, N.S.W.

Amphioplus (Amphioplus) stenaspis H. L. Clark, 1938 (Fig. 1b, c)

See : H. L. Clark, 1946 : 206 ; A. M. Clark & Rowe, 1971 : 101, fig. 53c–e.
D38 – 1(no disc) ; K6 – 1.

A new record for the Great Barrier Reef Province. The species was previously known only from Darwin.

Comparative remarks with *A. didymus* are given under that heading.

Amphioplus (Lymanella) bocki Koehler, 1910 (Fig. 1d–f)

See : Devaney, 1974 : 106.
Low Is : (L5) – 1 ; (L6) – [1] ; (L7) – 1 ; Three Is (3.2) – 3.

These records provide an extension of range to Australian waters for this species, recently revived by Devaney from the synonymy of *Amphioplus* (*Lymanella*) *laevis* (Lyman). The species was previously known from Fiji, the Society Islands, the Tuamotu Archipelago and the Cook Islands, as well as from Marovo lagoon, Solomon Islands, collected by Gibbs in 1965 (unpublished).

A specimen from Three Isles has d.d. 5·5 mm and a.l. *c.* 70 mm, a ratio of *c.* 1 : 12. After about a year in alcohol some of the arm spines are still banded with brown and there is a brown spot in the centre of each oral shield ; otherwise the specimen is pale.

The disc scaling is rather fine with no distinct rosette ; the margin is distinctly angular. The radial shields are fully contiguous, length : breadth *c.* 3 : 1 and the length is about two-fifths of the disc radius, that is slightly smaller than shown in Koehler's photograph of 1927, but conforming with the range in Devaney's material.

The oral shields are spearhead-shaped, longer than broad, with a short distal lobe and a sharp proximal angle.

The dorsal arm plates are broad elliptical, the distal side straight to convex with no trace of a median angle (Fig. 1e). The ventral arm plates are pentagonal with the distal side straight. The arm spines number three throughout ; beyond the arm base the second one becomes flattened with the tip abruptly truncated. The two tentacle scales are very large, the one on the ventral arm plate sometimes extending distally beyond the plate.

The complete absence of any sort of median distal angle to the dorsal arm plates and the bluntness of the middle arm spine fully justify Devaney's restoration of *A. bocki* from the synonymy of *A. laevis*, provisionally recorded here from Australian waters, which has conspicuously slender, sharp pointed arm spines. There is clearly some variation in the degree of modification of the second arm spine in *A. bocki.* Koehler describes the spines as obtuse and rounded at the tips, the middle one being evidently not distinguished ; Devaney's from SE Polynesia are bluntly pointed, the middle spine widest, which description agrees with the two specimens from the Solomon Islands (Fig. 1f). The spatulate form of the middle spine in these Queensland specimens (Fig. 1d) therefore appears to be excessive but does not on its own justify a taxonomic distinction.

Amphioplus (Lymanella) depressus (Ljungman, 1867)

See : H. L. Clark, 1946 : 205.
D1 – 1 ; D2 – 1 ; D6 – 1 ; D8 – 1 ; D19 – 1[1] ; K3 – 1 ; K8 – 2.

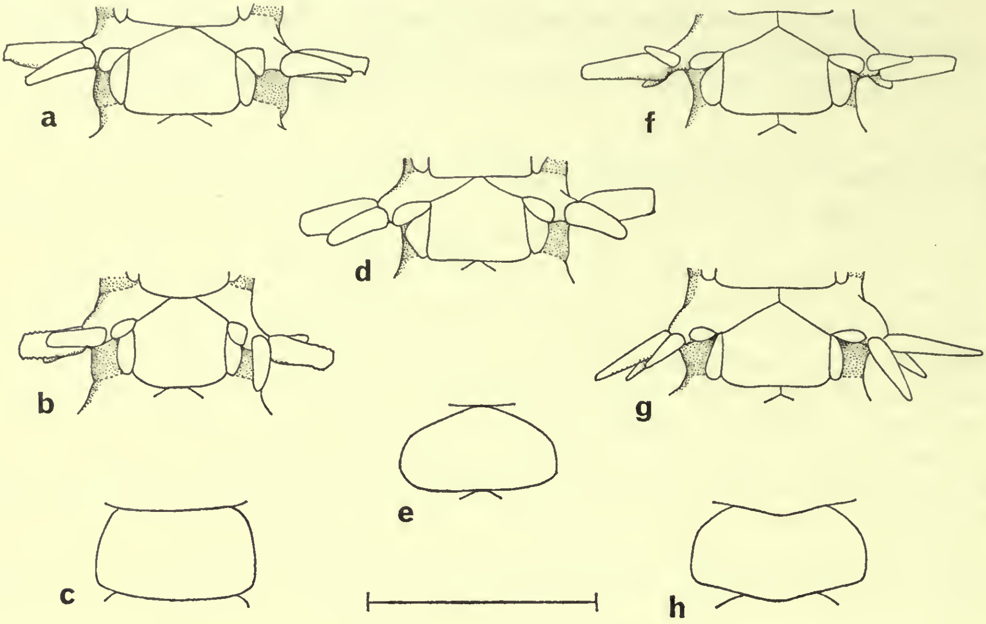

FIG. 1. Twentieth arm segments of *Amphioplus* species. (a) *Amphioplus* (*Amphioplus*) *didymus* H. L. Clark, d.d. *c.* 4 mm (actual disc lost), st. D15, ventral view. (b) and (c) *Amphioplus* (*Amphioplus*) *stenaspis* H. L. Clark, d.d. 3·8 mm, st. K6, ventral view (b) and the corresponding dorsal arm plate (c). (d) and (e) *Amphioplus* (*Lymanella*) *bocki* Koehler, d.d. 5·5 mm, Low Is, ventral view (d) and the corresponding dorsal arm plate (e). (f) *Amphioplus* (*Lymanella*) *bocki* Koehler, d.d. 6·0 mm, Marovo lagoon, Solomon Is, ventral view. (g) and (h) *Amphioplus* sp. ? *A.* (*Lymanella*) *laevis* (Lyman), d.d. *c.* 5 mm (actual disc lost), st. K2, ventral view (g) and the corresponding dorsal arm plate (h). [The scale represents 1 mm.]

These appear to be the first records of *Amphioplus depressus* from south of Torres Strait.

D.d. in the largest specimen seen by H. L. Clark from Australian waters is 6 mm. One of the present collection has the disc 1 mm broader.

Amphioplus sp. ? **A. (Lymanella) laevis** (Lyman, 1874) (Fig. 1g, h)

See : A. M. Clark & Rowe, 1971 : 102, fig. 48b, c.
K2 – 2(no discs).

The slight median angle on the dorsal arm plates, relatively slender pointed arm spines and less exaggeratedly large tentacle scales than usual in *Lymanella* leave little doubt of the identity of these two specimens, but it should be confirmed by intact specimens with radial shields before the range of the species can definitely be extended to Australia. *A. laevis* was previously known from the Red Sea to the Philippines, the Gilbert Islands and various localities in the East Indies, besides also being taken at Marovo lagoon, Solomon Islands, with *Amphioplus* (*Lymanella*) *bocki* by Gibbs in 1965.

Amphioplus sp. aff. ***A. (Amphioplus) pectinatus*** Mortensen, 1933

K10 – 1.

This small delicate specimen does retain the disc, though it is partly detached. The identification is only provisional on two counts, firstly because *Amphioplus pectinatus* is only known from as far away as Natal, South Africa, and secondly because there appear to be two distinct forms there, designated A and B by A. M. Clark (1974 : 456) and it is not yet certain to which one the holotype belongs.

D.d. in this specimen is *c.* 4·5 mm. The disc scaling is fairly fine, the radial shields are very long and narrow and barely contiguous distally, the oral shields are pear-shaped, the adorals only contiguous interradially on the jaw with the madreporic oral shield, the dorsal arm plates thin and broad fan-shaped, the arm spines slender and tapering, numbering four or five proximally for a few segments, then three, the second from lowest developing a small, distally directed hook and the tentacle scales numbering two, moderate in size. These characters conform with those of *A. pectinatus* but none of them are particularly distinctive, even in combination. However, the specimen also has two unusual features : there are spinose processes distal to each radial shield and there is a second oral tentacle scale on the side of the oral plate on the same level as the usual scale above (behind) the two middle oral papillae. The former occurs in both forms of *A. pectinatus* but the latter only in form B (A. M. Clark, 1974, fig. 8f–i).

Amphipholis squamata (Delle Chiaje, 1829)

See : H. L. Clark, 1946 : 202.

D5 – 1 ; D6 – 1 ; D46 – 2 ; D47 – 1.

Amphiura (Amphiura) ambigua Koehler, 1905

See : Koehler, 1905 : 39 ; H. L. Clark, 1946 : 196.

K10 – 1.

This is a new record for the Great Barrier Reef Province, though a specimen from Port Curtis in the British Museum collections is now also identified as *Amphiura ambigua.* The species was previously known in Australia from Darwin (H. L. Clark, 1938).

The K10 specimen has d.d. only 3 mm ; all the arms are badly broken. The distal oral papilla is small and peg-like, there are seven arm spines proximally, the lowest and uppermost spatulate, the second and third from lowest bihamulate and the others with only distally pointing hooks and there are two large tentacle scales. These characters agree with Koehler's description of the holotype of *A. ambigua*, from the Sulu Archipelago, Philippines, but not the ventral side of the disc which is naked, not scaled. However, in this it agrees with H. L. Clark's key, although he does not mention the anomaly elsewhere ; presumably his Darwin specimens are partly naked. In contrast, the Port Curtis specimen has fine scaling both dorsally and ventrally; d.d. is 6 mm and there are eight arm spines, the middle ones hooked; the distal oral papilla is relatively larger and more rounded than in the smaller specimen.

Several species of amphiurids are already known to show considerable variation in the extent of the disc scaling, notably *Amphiura acrystata* H. L. Clark, 1911, from the North Pacific, so this character alone is no barrier to considering ventrally naked Australian specimens to be conspecific with *A. ambigua*.

Amphiura (Amphiura) bidentata H. L. Clark, 1938

See: H. L. Clark, 1946: 197.
K3 – 2.

Amphiura (Amphiura) catephes H. L. Clark, 1938

See: H. L. Clark, 1946: 193.
D2 – 1; D6 – 1.

This is a new record for the Great Barrier Reef Province. The species was previously known only from two specimens taken at Port Jackson, N.S.W.

Amphiura (Amphiura) constricta Lyman, 1879

See: H. L. Clark, 1946: 194.
D16 – 1; D46 – 1.

Amphiura (Amphiura) diacritica H. L. Clark, 1938

See: H. L. Clark, 1946: 196.
Low Is. (L6) – 1.

The holotype and only other recorded specimen was taken at Black Island, Whitsunday Group (H. L. Clark, 1938). The Low Isles specimen was found in muddy sand at low water mark.

Amphiura leptotata H. L. Clark, 1915

See: A. M. Clark & Rowe, 1971: 95, fig. 50a–c.
D1 – 2; D2 – 3; D11 – 2; D16 – 2; D21 – [2]; D23 – 3; D34 – 1; D39 – 1; D48 – 1; D49 – 1.

These records extend between 14°21′S and 16°40′S and provide an extension of range to Australia. The type-locality is in the Philippines and the species was also collected by Gibbs at Marovo lagoon, Solomon Islands, in 1965. It may have escaped attention because of the small size, d.d. in the holotype being only 3·5 mm and not exceeding 3 mm in the other specimens.

At d.d. 3 mm the arm length is 30+ mm. The disc is covered with very fine scales above but on the ventral side this gives way proximally to naked skin with only scattered scales, appearing dark brown in colour. The radial shields are banana-shaped, two-fifths to half as long as the disc radius and with length : breadth *c.* 3 : 1 ; they are completely separated by a row of four or five scales.

The arm spines number four proximally, falling to three. The second spine from below is much broader than the others with an abruptly truncated tip, not simply tapering to a blunt tip. There are no tentacle scales.

The absence of tentacle scales distinguishes this species from all those included in H. L. Clark's key to the Australian species of *Amphiura*. However, with the partially bare underside of the disc it is shared by a species which H. L. Clark (1946 : 201) referred to *Ophionephthys*, namely *Ophiolepis perplexa* Stimpson, 1855, from Port Jackson, referred by Lyman in 1865 to *Amphiura*, to which it should be restored following A. M. Clark's restriction of *Ophionephthys* (1970). *Amphiura perplexa* does not appear to have been recorded from the Port Jackson area since 1855. If further material from N.S.W. proves to be conspecific with that from Queensland, then the name *Amphiura leptotata* must become a synonym.

Amphiura (Amphiura) magnisquama H. L. Clark, 1938

See : H. L. Clark, 1946 : 195.
D17 – 1.

This is a new record for the Great Barrier Reef Province. The species was previously known from off Botany Bay, N.S.W. (H. L. Clark, 1938).

Amphiura phrixocantha sp. nov.

(Fig. 2, Pl. 1, figs 1–3)

TYPE MATERIAL. D36 – 2. 15°45′S : 145°33′E (between Endeavour and Cairns Reefs, opposite Papuan Pass) at 37 m depth. Holotype B.M. reg. no. 1975.6.27.44 ; paratype Queensland Museum no G. 9297.

DESCRIPTION. The holotype has d.d. 8 mm, a.l. 30+ mm. The arms taper rather abruptly distally ; two of them are regenerating.

The disc is covered with relatively large, very thick scales, numbering five to seven across each interradius between adjacent radial shields. No primary rosette is distinguishable. The disc is strongly contracted interradially and on the ventral side and this probably accounts for the almost vertical alignment of the ventral scales. The radial shields are markedly convex abradially, 1·9–2·0 mm in length, with length : breadth *c.* 2·0 : 1 and length about half the disc radius. The two of each pair are completely separated by three (or in one case four) large scales.

The oral shields are keyhole-shaped, the main part almost circular but with a well-developed distal lobe ; length : breadth is 1·5 : 1. The adoral shields are broadly contiguous interradially with a rounded end radially ; from the middle half of the proximal side of each arises a relatively huge, very broad rounded distal oral papilla, about as long as the oral plate and about half again as broad, sometimes slightly prolonged interradially towards the block-like infradental papillae. The first oral tentacle scale is compressed vertically and appears very narrow and pointed in ventral view. A most unusual additional scale borders the adradial side of the second (more superficial) oral tentacle pore like a vertical crest, its ventral end curling horizontally to a small extent just behind the large distal oral papilla, so giving the effect of a small conical additional oral papilla. It probably arises from the edge of the first ventral arm plate.

The dorsal arm plates are relatively narrow, covering only the midline of the arms, rounded octagonal in shape and broadly contiguous, the distal edge straight or slightly convex, about as broad as long proximally but becoming half as broad again by the twentieth segment. The ventral arm plates are broader than long, rectangular, with blunt distal corners, the proximal and distal sides straight.

The number of arm spines is nine proximally, falling to seven by the thirtieth segment but still as many as five on the distalmost segments remaining. Except for the three uppermost, which are simply flattened and blunt, and the lowermost one, which is pointed, all the spines are elaborately hooked, hence the specific name. The hooks are glassy and hyaline. The second from lowest spine is the longest and on the basal segments has a large hook directed proximally; beyond the disc it becomes bihamulate. The next three spines are mostly also bihamulate but the sixth usually has only the distal-pointing hook.

The tentacle scales are unusual. On the first four arm segments there are two large scales on each pore, a rounded proximal one on the lateral arm plate overlying a more elongated but truncated scale projecting at right angles from the side of the ventral arm plate. From about the fifth arm segment, the latter scale becomes gradually reduced in size and inset so as to become barely distinguishable from about the twelfth segment.

The paratype has d.d. *c* 5·5 mm. The disc is again very contracted interradially. The rosette is distinct among the large rounded scales. Proximally there are not

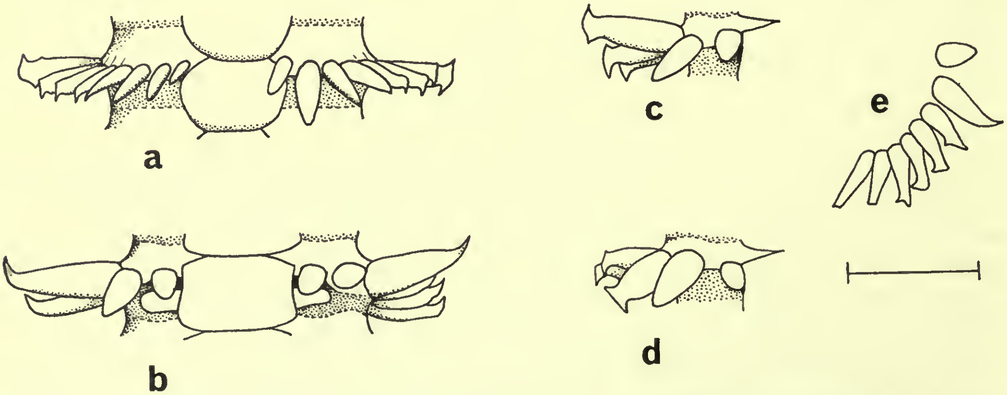

FIG. 2. *Amphiura phrixocantha* sp. nov. Holotype. (a) Twelfth arm segment in dorsal view. (b) Fifth segment in ventral view. (c) and (d) Parts of twelfth and twenty-fifth segments in ventral view. (e) Oblique distal ventrolateral view of seventh arm segment, the lower spines (shown uppermost in the figure) somewhat foreshortened. [The scale represents 1 mm.]

more than six arm spines. Otherwise it is similar to the holotype, allowing for the smaller size.

Both specimens, after about a year in alcohol, still show a yellow colour on the dorsal arm plates, interrupted at intervals by usually one to three unpigmented plates.

AFFINITIES. This species has most in common with *Amphiura dolia* H. L. Clark, 1938, from Port Jackson, to which it runs down in H. L. Clark's *Amphiura* key of 1946 (p. 191) since it has two tentacle scales, fully scaled disc with coarse scales and numerous arm spines. The very broad distal oral papilla is shared by both, while the disc scaling is also thick and the form of the radial shields similar in *A. dolia*, allowing for the much larger size of the holotype, d.d. 11–12 mm. However, the arm spines are still only up to eight in number at this large size and are unspecialized, 'pointed but not acute', also the second tentacle scale maintains its size, or even exceeds the proximal scale.

Amphiura (Fellaria) octacantha (H. L. Clark, 1915)

See : H. L. Clark, 1946 : 200 (as *Ophionephthys octacantha*) ; A. M. Clark & Rowe, 1971 : 95, fig. 26b (as *Amphiura* (*Fellaria*) *octacantha*).

SYNONYM : *Ophionephthys decacantha* H. L. Clark, 1938.

K3 – 2.

Previous records : Torres Strait.

Dougaloplus echinatus (Ljungman, 1867)

See : H. L. Clark, 1946 : 203 (as *Ophiocnida echinata*) ; A. M. Clark & Rowe, 1971 : 100 (as *Dougaloplus echinatus*).

D3 – 1 ; D23 – [1] ; D27 – 1.

Previous record : Papuan Pass (1 specimen) (H. L. Clark, 1932).

Ophiocentrus verticillatus (Döderlein, 1896)

See : H. L. Clark, 1946 : 198.

D6 – 1.

A new record for the Great Barrier Reef Province. Previously the species was known from Broome, NW Australia.

OPHIACTIDAE

Ophiactis savignyi Müller & Troschel, 1842

See : H. L. Clark, 1946 : 210.

Turtle I I. (reef flat) – 7.

Ophiactis sp. juv.

D4 – 1 ; D6 – 2 ; D16 – 1.

OPHIOTRICHIDAE

Macrophiothrix belli (Döderlein, 1896)

See : H. L. Clark, 1946 : 221.
Mid Reef (reef flat) – 1 ; Turtle IV I. (reef flat) – 1.
Previous record : Torres Strait.

Macrophiothrix koehleri A. M. Clark, 1968

See : Koehler, 1907 : 333 (as *Ophiothrix galatheae* [part]) ; H. L. Clark, 1932 : 204 (as *Ophiothrix longipeda* [part]) ; A. M. Clark & Rowe, 1971 : 114, fig. 37p (as *Macrophiothrix koehleri*).
Three Is (reef flat) – 2; Three Is (3.11) – 1.

In H. L. Clark's key to the species of *Macrophiothrix* (1946 : 218) this species runs down to the vicinity of *M. spinifera* and *M. scotia* (EE) because of the presence of spinelets on its oral shields, whereas its arm structure agrees far better with that of *M. belli*, the dorsal arm plates having sharp latero-distal angles and the longer arm spines smooth shafts and clavate tips.

Previous records : Probably Koehler's specimen from Torres Strait as well as H. L. Clark's Barrier Reef Expedition one from Low Isles are conspecific with *M. koehleri*.

Macrophiothrix lorioli A. M. Clark, 1968

See : A. M. Clark & Rowe, 1971 : 115, fig. 37 m.
Mid Reef (reef flat) – 1.

This specimen provides a new record for Australian waters. The species was previously known from the South China Sea, the Solomon Islands and the Tonga Islands.

In H. L. Clark's 1946 key, *M. lorioli* runs down to the vicinity of *M. callizona*, *M. calyptaspis* and *M. michaelseni* (GG) because of the unarmed oral shields and non-trapezoidal dorsal arm plates, these being fan-shaped with more or less distinct lateral angles. *M. callizona* differs in having elliptical dorsal arm plates and the distal side of the ventral arm plates concave rather than convex. *M. calyptaspis* has the arms relatively short, less than ten times the disc diameter rather than 14–19 times in *M. lorioli* (17·5 times in this specimen), while *M. michaelseni* from the west coast of Australia (as opposed to the north-west) has the radial shields more or less bare rather than covered with trifid stumps.

Macrophiothrix megapoma H. L. Clark, 1938

See : H. L. Clark, 1946 : 219.
D16 – 1.

Macrophiothrix sp. aff. ***M. longipeda*** (Lamarck, 1816)

See : H. L. Clark, 1946 : 221.
D21 – 1.

This specimen agrees in all respects with *M. longipeda* except that it has the lowermost arm spine hook-shaped with only one or two accessory spines within the main hook, rather than comb-like with multiple accessory spines. There are also only up to six arm spines (d.d. is 15 mm), an unusually small number for *M. longipeda*.

Ophiomaza cacaotica Lyman, 1871

See : H. L. Clark, 1946 : 234.
D7 – 1 (on crinoid *Comatula rotalaria*).

H. L. Clark (1921) records this commensal (or parasitic) ophiuroid from *Comatula purpurea* and *Comanthus annulatus* (i.e. *Comanthus parvicirrus*). Other specimens in the British Museum collections from Queensland were from *Comatula solaris*, *Comantheria perplexa* and *Zygometra microdiscus*.

Ophiothela danae Verrill, 1869

See : H. L. Clark, 1946 : 229 (as *Ophiothela hadra*) ; A. M. Clark & Rowe, 1971 : 116, pl. 14, fig. 5.
South-west of Long Reef at 15°05·2′S : 145°33·0′E (Grab st. 314A), 31 m depth – innumerable specimens on a gorgonian [5].

The arm length in these specimens appears to be 3·5–5·0 times the d.d., their colour in alcohol is blue on white (the gorgonian contrasts in vermilion but the match may have been better in life) and morphologically also there is no reason why they should not be referred to *O. danae*, with which A. M. Clark provisionally synonymized *Ophiothela hadra* in 1971. Although H. L. Clark (1915) originally distinguished *O. hadra* by the arms being only about twice the d.d., in 1946 he amended this to 'hardly' four times the d.d. It is possible that relative arm length may be correlated with the nature of the host, the types of *O. hadra* being from a sponge where shorter arms may be at an advantage. This remains to be seen from field studies, when the extent of correlation between ophiuroid and the colour of the host can also be determined, following from Japanese work on these lines.

Ophiothrix (Ophiothrix) foveolata Marktanner-Turneretscher, 1887

See : A. M. Clark & Rowe, 1971 : 110, pl. 15, fig. 3.
D28 – 2 ; D51 – 3.

These records represent an extension of range to Australia. The species was previously known from the Aru and Kei Islands, the Sunda Islands and Sulu Archipelago.

Because of the completely bare radial shields and arms of moderate length, *O. foveolata* runs down to *Placophiothrix* s.l. in H. L. Clark's key to the Ophiotrichidae (1946 : 213). The very pretty colour pattern with the radial shields and distal ends of the arm segments (ventrally as well as dorsally) outlined by narrow bands (dark-red in preserved specimens) serves to distinguish it from the species which H. L. Clark included in *Ophiothrix* and *Placophiothrix* while the narrowly contiguous dorsal arm plates exclude it from *Placophiothrix*. The disc armament is relatively reduced dorsally with only a few scattered spinelets.

Four of these specimens have d.d. *c.* 6 mm and the arm length 5·0–6·7 times as much, while the fifth at d.d. 4 mm has arms 30 mm long, a ratio of 1 : 7·5.

Ophiothrix (Acanthophiothrix) armata Koehler, 1905

See : H. L. Clark, 1932 : 205 (part, st. 25) (as *Ophiothrix stelligera*) ; A. M. Clark & Rowe, 1971 : 84, 90, 111 (*as Ophiothrix* (*Acanthophiothrix*) *armata*).
South-east of Long Reef at 15°04·6′S : 145°37·2′E (Grab st. 315A) at 31 m depth – 2 (on coral *Seriatopora*) ; D45 – 1.
Previous record : Papuan Pass (1 specimen) (H. L. Clark, 1932).

Since H. L. Clark (1932) did not distinguish the small Barrier Reef Expedition specimen from *Ophiothrix stelligera* (i.e. *O. ciliaris*), *Ophiothrix armata* is not included in his keys of 1946. It would fall within *Placophiothrix* in his wide sense, because of the conspicuous, mostly bare radial shields. In the *Placophiothrix* key (1946 : 223) it runs down to EE, *P. elegans* (with a single longitudinal dark line on each arm) and *P. trilineata*, said to have three dark lines separated by two light ones. However, this last observation is surely a mistake since other descriptions of *trilineata*, which A. M. Clark has referred back to *Ophiothrix* s.s., give three *light* lines and two dark ones between them, the limits of the outer light ones sometimes irregular or ill-defined.

All four specimens from the Great Barrier Reef are small with slender arms and needle-like spines, the arms being marked with two dark lines without a background of lighter colour.

Ophiothrix (Acanthophiothrix) proteus Koehler, 1905

See : A. M. Clark & Rowe, 1971 : 111, pl. 15, fig. 5.
K6 – 1.

This record provides an extension of range to Australia. The species has previously been recorded in the Pacific from the South China Sea, the Sunda Islands, Kei Islands and New Caledonia.

The single specimen belongs to the colour form of *O. proteus* which has the double dark lines on each arm green rather than purple, though the radial shields and central disc plates are still pinkish after preservation in alcohol ; the keel of the dorsal arm plates between the green lines is white. The longest arm spine is five to six times the segment length.

Like the species above, *O.* (*Acanthophiothrix*) *proteus* is likely to run down to section EE of H. L. Clark's 1946 key to the species of *Placophiothrix*. Again it is a much more slender species than *trilineata*.

Ophiothrix (Acanthophiothrix) purpurea von Martens, 1867

See : A. M. Clark & Rowe, 1971 : 112, fig. 35d, pl. 15, figs 4, 11.
D16 – 1.

This record provides an extension of range to Australian waters. The species has previously been recorded through most of the Indo-West Pacific, including the Banda Sea, New Hebrides and Solomon Islands in the neighbourhood of Australia.

The specimen is small with d.d. only *c.* 1·5 mm but has the distinctive narrow dark line on each arm and very slender form. Again it runs down to section EE of H. L. Clark's *Placophiothrix* key but differs from *P. elegans*, which A. M. Clark has referred back to *Ophiothrix* s.s., recorded from Disaster Bay, N.S.W., in the narrow hexagonal rather than broad rhombic dorsal arm plates and more needle-like armament.

Ophiothrix (Keystonea) propinqua Lyman, 1861

See : H. L. Clark, 1946 : 232 (as *Ophiotrichoides propinqua*) ; A. M. Clark & Rowe, 1971 : 107, pl. 15, fig. 7 (as *Ophiothrix* (*Keystonea*) *propinqua*).
K4 – 1.
Previous record : Murray Is (H. L. Clark, 1946).

Ophiothrix (Theophrix) pusilla Lyman, 1874

See : A. M. Clark & Rowe, 1971 : 107, fig. 35c, pl. 15, fig. 8.
D6 – 1 ; D36 – 1 ; K3 – 1.

These records provide an extension of range to Australian waters. The species has previously been recorded from the South China Sea, Philippines, Sunda and Kei Islands.

The three specimens have d.d. 2·6–3·5 mm and d.d. : a.l. 1 : 2·3–3·7, the relative length increasing with size. The colour in alcohol is pale with a bluish tinge and faint blue irregular bands on the arms.

This is a small but distinctive species with its thick, elongate, oval dorsal arm plates, much narrower than long, relatively short arm spines not exceeding twice the segment length and complete covering of the disc including the radial shields with trifid stumps. The structure and shortness of the arms serve to distinguish it from all the species included in H. L. Clark's key for *Ophiothrix* (1946 : 214).

OPHIOCOMIDAE

Ophiarthrum elegans Peters, 1851

See : H. L. Clark, 1946 : 252.
Mid Reef (reef flat) – 8[2] ; Three Is (reef flat) – 2 ; K4 – 1.

Ophiocoma dentata Müller & Troschel, 1842

See: H. L. Clark, 1946: 246 (as *Ophiocoma insularis* var. *variegata*); Endean, 1953: 55; 1956: 126 (both as *O. insularia* var. *variegata*); A. M. Clark & Rowe, 1971: 119 (as *O. dentata*).
Mid Reef (reef flat) – 8[1]; Lark Passage (reef flat) – 2.

Ophiocoma erinaceus Müller & Troschel, 1842

See: H. L. Clark, 1946: 244.
Turtle IV I. (reef flat) – 1.

Ophiocoma scolopendrina (Lamarck, 1816)

See: H. L. Clark, 1946: 243.
Three Is (reef flat) – 7[1]; Lark Passage (reef flat) – 1.

Ophiocomella sexradia (Duncan, 1887)

See: H. L. Clark, 1946: 206 (as *Amphiacantha sexradia*) and 247 (as *Ophiocoma parva*); A. M. Clark & Rowe, 1971: 118, fig. 38c–f (as *Ophiocomella sexradia*).
Turtle I I. (reef flat) – 1.
Previous records: Mer, Murray Is [also Lord Howe I.] (H. L. Clark, 1946).

OPHIONEREIDAE

Ophionereis dubia (Müller & Troschel, 1842)
See: H. L. Clark, 1946: 240 (as *Ophionereis stigma* and *O. dubia*).
D3 – 1; D6 – [1]; D19 – 1.

As noted in 1953 (*Proc. zool. Soc. Lond.* **123**: 82) although H. L. Clark's supposition that the 'Alert' specimens from Torres Strait named *Ophionereis dubia* by Bell are in fact *O. semoni* (Döderlein) is largely correct, two of them do have the disc scaling, oral shields and proximal ventral plates unobscured by skin and the arm spines relatively long, thereby justifying the inclusion of *O. dubia* in the Australian fauna even if it were not for the inclusion of the north-western Australian *Ophionereis stigma* H. L. Clark in the synonymy.

The present records extend the range south from Torres Strait.

Ophionereis porrecta Lyman, 1860

See: H. L. Clark, 1946: 238.
K4 – 1.
Previous record: Murray Is (H. L. Clark, 1921).

Ophionereis semoni (Döderlein, 1896)

See : H. L. Clark, 1946 : 240.
D47 – 1 ; K3 – 4[2].
Previous records : Lindeman I., near Mackay (H. L. Clark, 1938) ; east of Snake Reef (H. L. Clark, 1932) ; Low Is (Endean, 1956).

OPHIODERMATIDAE

Ophiarachna incrassata (Lamarck, 1816)

See : H. L. Clark, 1946 : 253.
Watson I. (reef flat) – 1 ; Mid Reef (reef flat) – 2.

Ophiarachnella gorgonia (Müller & Troschel, 1842)

See : H. L. Clark, 1946 : 260.
Mid Reef – 4[1].

Ophiarachnella infernalis (Müller & Troschel, 1842)

See : H. L. Clark, 1946 : 262.
D27 – 1 ; D51 – 1.

Ophiochaeta hirsuta Lütken, 1869

See : A. M. Clark & Rowe, 1971 : 127, fig. 44a, b.
D6 – 1.

This record provides an extension of range to Australian waters. The species has previously been recorded from Fiji and the Gilbert Islands and there are specimens in the British Museum collections from Aldabra (Indian Ocean) and Tetel (or Gaskell) Island in the Solomon Islands (collected by Dr H. G. Vevers in 1965).

Though small (d.d. 4 mm) the specimen shows the mixture of extremely fine spinelets and indented granules on the disc and the spiniform rather than granuliform armament of the oral plates, which serve to distinguish *Ophiochaeta hirsuta* from all the ophiodermatids included in H. L. Clark's key (1946 : 252). The arm spines are short and appressed and the oral shields are bare. Unusually in this specimen the radial shields are also bare but this may be a juvenile character. The colour in alcohol consists of a light brown central area on the disc bordered with dark brown and then a white peripheral area ; ventrally the disc and arm bases are white but the rest of the arms are banded with brown on both sides.

Ophiochasma stellatum (Ljungman, 1867)

See : H. L. Clark, 1946 : 259.
D21 – 1 ; D26 – 3 ; D27 – [1] ; K3 – 2[1].

Ophiopeza spinosa (Ljungman, 1867)

See : H. L. Clark, 1946 : 258 (as *Ophiopezella spinosa*) ; A. M. Clark & Rowe, 1971 : 127, fig. 44e (as *Ophiopeza spinosa*).
K5 – 1 ; K6 – 1.
Previous records : Torres Strait ; Murray Is (H. L. Clark, 1921).

Ophiopsammus yoldii (Lütken, 1856)

See : H. L. Clark, 1946 : 257 (as *Pectinura yoldii*) ; A. M. Clark & Rowe, 1971 : 127, pl. 21, figs 7, 8 (as *Ophiopsammus yoldii*).
K3 – 11[2].

Ophiodermatid sp. juv.

K3 – 1.

OPHIURIDAE

Ophiolepis superba H. L. Clark, 1915

See : H. L. Clark, 1946 : 272.
Two Is (reef flat) – 3.

Ophiura kinbergi (Ljungman, 1867)

See : H. L. Clark, 1946 : 270.
D21 – 1 ; D23 – 1 ; D29 – 2[1] ; D31 – 5.
Previous record : Murray Is (Endean, 1957).

Class *ECHINOIDEA*

CIDARIDAE

Prionocidaris bispinosa (Lamarck, 1816)

See : H. L. Clark, 1946 : 286.
D17 – 3[1].

DIADEMATIDAE

Diadema setosum (Leske, 1778)

See : H. L. Clark, 1946 : 297 (as *Centrechinus setosus*) ; Endean, 1956 : 127 (as *Diadema setosum*).
Two Is (reef flat) – 1 ; Three Is (reef flat) – S.

TEMNOPLEURIDAE

Mespilia globulus (Linnaeus, 1758)

See : H. L. Clark, 1946 : 315.
Turtle I I. (reef flat) – 1 ; D50 – 5[1] ; K6 – 1.
Previous records : Port Denison (Mortensen, 1943) ; Trinity Bay (off Cairns) (Tenison-Woods, 1880b) ; Low Is ; Hardy Reef ; Heron I. (Endean, 1961).

Temnopleurus alexandri (Bell, 1884)

See : H. L. Clark, 1946 : 311 (as *Salmacis virgulata* var. *alexandri*) ; Endean, 1956 : 128 (as *Temnopleurus alexandri*).
D1 – 1.

Temnotrema phoenissa H. L. Clark, 1926

See : H. L. Clark, 1946 : 314.
D50 – 1.

This small echinoid, h.d. (horizontal diameter) 15 mm, v.d. 10 mm, is still very distinctively coloured in alcohol. The apical system is greenish, the test aborally dark purplish-red, darker in the interambulacral areas, the aboral spines red with white tips and the primary ones also with white bases ; orally the test is white and the spines pale green. This combination of colours agrees not only with that of the holotype and only recorded specimen of *Temnotrema phoenissa* from Ellison Reef (h.d. only 6·5 mm) but also with *Temnotrema pulchellum* (Mortensen), known from the Philippines to the Kei Islands. Mortensen (1943 : 268) has already suggested that the two nominal species may prove to be conspecific. Without material of *T. pulchellum* to hand this problem cannot be resolved.

Temnopleurid sp.

D4 – 1 ; D39 – 3.

TOXOPNEUSTIDAE

Gymnechinus epistichus H. L. Clark, 1912

See : H. L. Clark, 1946 : 326.
D21 – 1.

Tripneustes gratilla (Linnaeus, 1758)

See : H. L. Clark, 1946 : 326.
Three Is (reef flat) – 1.

PARASALENIIDAE

Parasalenia sp.

K4 – 1 (test only and therefore not positively identifiable).

ECHINOMETRIDAE

Echinometra mathaei (de Blainville, 1825)

See : H. L. Clark, 1946 : 332.
Three Is (reef flat) – 2.

ECHINONEIDAE

Echinoneus abnormalis de Loriol, 1883

See : A. M. Clark & Rowe, 1971 : 158.
K4 – 1.

This record provides an extension of range to Australia. The specimen differs from *Echinoneus cyclostomus* Leske, 1778, known from Low Isles and Heron Island (Endean, 1956) and from Lord Howe Island (H. L. Clark, 1938), in having the spine tubercles perforated and in lacking glassy knobs on the test. *E. abnormalis* has previously been recorded from Mauritius (the type locality), the Kei Islands, Rotuma in the Ellice Islands, Palmyra Island and the Hawaiian Islands ; there is also a specimen in the British Museum collections from Aldabra. Since the species is sympatric in most, if not all, of these localities with the much more common *E. cyclostomus*, it is possible that *E. abnormalis* may have gone unrecognized in other samples.

FIBULARIIDAE

Fibularia ovulum Lamarck, 1816

See : A. M. Clark & Rowe, 1971 : 161, 167.
K7 – 1.

This record represents an extension of range to Australia. The species has previously been recorded from most parts of the tropical Indo-West Pacific except from the more remote Pacific islands.

Although Mortensen (1948) reckons that most of H. L. Clark's records of *Fibularia craniolaris* (Leske, 1778) are conspecific with *Fibularia ovulum*, he makes an exception of the Australian ones, referring them instead to *Fibularia oblonga* Gray, 1851, which he recorded from 'South, West and North Australia', without precise localities (1948 : 223). However, in H. L. Clark's key to the Australian species of *Fibularia* (1946 : 347) the present specimen does tend to run down to *F. craniolaris* on account of its high ovoid test (length : height 4·5 : 3·5 mm) and the rounded pores forming distinct petals on the aboral side (though they are not appreciably smaller than the genital pores). In these same characters it also agrees with *F. oblonga*, recorded by Endean (1961 : 294) from Caloundra, southern Queensland, but in intact specimens like this one, as opposed to dead tests, there are important differences in the plating of the peristome and periproct. In *F. ovulum* the peristomial membrane is devoid of plates and the periproct has five triangular plates, as this specimen shows, whereas *F. oblonga* has multiple small irregular plates in both peristome and periproct. However, dead tests of *F. ovulum* should be recognizable as having the round or quadrangular periproct as broad as or broader than long, whereas in *F. oblonga* it is normally elongate oval.

According to H. L. Clark the common *Fibularia* in northern Australia is *F. volva* Agassiz & Desor, 1847, which should be distinguishable from both *F. ovulum* and *F. oblonga* by the relatively low test (length : height *c.* 2 : 1) with more or less tapering ends.

Fibulariid sp.

D37 – 2 (tests only).

LAGANIDAE

Laganum decagonale (de Blainville, 1827)

See : A. M. Clark & Rowe, 1971 : 162.
D41 – 1.
Previous records : Torres Strait (Agassiz, 1881) ; Bowen (Mortensen, 1948).

This species was excluded from the Australian fauna by H. L. Clark (1946) although in 1925 (p. 156) he cited a *Challenger* specimen of *Laganum decagonale* from Torres Strait, following Agassiz. There are now a total of eight *Challenger* laganids from Torres Strait in the British Museum collections, some acquired since 1925. Although they show considerable variation in the number and development of the genital pores and the shape of the test, several of them agree with Mortensen's description of *L. decagonale* (1948 : 331) in having five genital pores and an S-shaped groove for the madreporic pores on the apical system, both characters distinguishing them from *Peronella*. However, the extent of the variation throws some doubt on the generic weight of these characters. The remaining *Challenger* specimens bridge the gap with, and may even run down to, *Peronella lesueuri* (Valenciennes, 1841) to which H. L. Clark (1946 : 346) referred them.

Laganum depressum Lesson *in* L. Agassiz, 1841

See : H. L. Clark, 1946 : 343 (*Laganum depressum*) and 344 (*Laganum dyscritum*) ; Endean, 1956 : 129, 134 (*L. depressum*).
Low Is : (L5) – 5 ; (L6) – 4 ; D17 – 1 ; D27 – 1 ; D30 – [2] ; D31 – 1 ; D33 – 1 ; D41 – 1 ; D46 – 1.

This species is very common in muddy sand close to the Anchorage at Low Isles, as also noted by Endean (1956) who agreed with Mortensen (1948) that *Laganum dyscritum* H. L. Clark, 1932, of which Low Isles in the type locality, is synonymous with *Laganum depressum*. H. L. Clark had acknowledged the likelihood of confusion between the two but considered that those he called *L. dyscritum* have significantly broader tests, more posteriorly situated periprocts and relatively larger petaloid areas, besides having more elongated spinelets and a purplish brown coloration, rather than the yellowish-khaki usual in *L. depressum*. Mortensen attributed the colour difference to the type material of *L. dyscritum* possibly having been preserved together with comatulids and it is certainly true that most Queensland comatulids are very liable to release copious amounts of purple pigment in alcohol. None of the laganids collected at Low Isles by Gibbs are at all purple. The morphological differences Mortensen discounted as being within the range of variation of *L. depressum*. His conclusion is supported by a series of measurements made on the present collection together with the material from the Great Barrier Reef Expedition which H. L. Clark referred to both *L. depressum* and *L. dyscritum* as well as specimens of *L. depressum* from various other parts of its extensive Indo-Pacific range.

Although H. L. Clark recorded four specimens of *Laganum* from Low Isles as *L. depressum*, these are all large spineless tests, length 60 mm or more, and do not compare in size with the numerous specimens from Low Isles which he referred to *L. dyscritum* where length is 28–42 mm. The three Great Barrier Reef Expedition specimens from st. XXIV (NE of Pasco Reef) with length 32–45 mm are unfortunately not in the British Museum collections and must be either at Harvard or the Australian Museum. H. L. Clark's values for test breadth of *L. depressum* of 0·80–0·85 (or 80–85%) of length and *c.* 20% for distance of the periproct from the posterior edge of the test appear to have been taken from the two tests from the Anchorage area, now measured as 71 and 65 mm in length with breadths 79 and 89% and periproctal distance 19 and 18%. However, 30 specimens of *L. depressum* with test length *c.* 25–40 mm from various localities show a much greater breadth range, from 83–93% with a mean of 89%. This compares with a range of 80–94% and again a mean of 89% for 30 of the specimens which H. L. Clark named *L. dyscritum*, suggesting that his figure of 90–95% was biased and probably derived from only a few specimens. The mean periproctal distance also practically coincides when these two series are compared, nor is there a significant difference in the relative length of the petaloid area.

Laganid sp. juv.

K3 – 1 ; K8 – 1.

Peronella lesueuri (Valenciennes in L. Agassiz, 1841)

See : H. L. Clark, 1946 : 346.
K8 – 1.

Peronella orbicularis (Leske, 1778)

See : H. L. Clark, 1946 : 346.
D2 – 1 ; D7 – 2 ; D14 – 1 ; D16 – 1 ; D19 – 2 ; D36 – 1 ; D48 – 1 ; D49 – 1 ; D52 – [2] ; K2 – 2 ; K3 – 1.

Peronella sp. juv.

D1 – 1.

SPATANGIDAE

Maretia planulata (Lamarck, 1816)

See : H. L. Clark, 1946 : 380 (as *Maretia ovata*) [non *Spatangus ovatus* Leske, 1778] ; Endean, 1956 : 129 (as *Maretia planulata*).
Low Is (L5) – 15 ; Low Is (Anchorage at 3 m depth) – 2 ; D23 – 1 ; D26 – [1] ; D29 – 4 ; K1 – 6 ; K3 – 8[6].

Like *Laganum depressum* this species is common in muddy sand close to the Anchorage on Low Isles. During the period of exposure on day-time spring tides it often comes to the surface of the sand. This habit has also been noted in *Lovenia elongata* in the Red Sea and elsewhere.

LOVENIIDAE

Lovenia elongata (Gray, 1845)

See : H. L. Clark, 1946 : 381.
K7 – 1.

SCHIZASTERIDAE

Schizaster lacunosus (Linnaeus, 1758)

See : H. L. Clark, 1946 : 368.
Low Is (L2) – 1. South of Arlington Reef at 16°42·5′S : 145°57·0′E (Grab ARL 16) at 51 m depth – 1. [Both from muddy sand.]
Previous records : Torres Strait ; Turtle Is (H. L. Clark, 1946).

BRISSIDAE

Brissus latecarinatus (Leske, 1778) (Fig. 3b)

See : H. L. Clark, 1946 : 375.
Pelican I. (strand line) – 4 (tests only) ; D19 – 1.

One of the four specimens from Pelican Island agrees in some ways more with *Brissus agassizi* Döderlein, 1885, having the posterior end of the test vertically truncated, the posterior interambulacrum being only slightly carinate aborally and

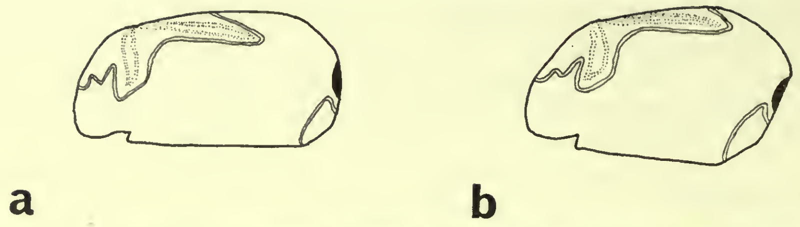

FIG. 3. Profiles of (a) *Brissus agassizi* Döderlein and (b) *B. latecarinatus*.

not prolonged backwards to overhang the periproct and conceal it from dorsal view (Fig. 3a), in contrast to *B. latecarinatus* (Fig. 3b). Endean (1956 : 129) records as '*Brissus* (? *latecarinatus*)' a dead test from Heron Island which approximates to some extent with this specimen, lacking the overhang above the periproct, though it does have the posterior end of the test 'obliquely truncate as in typical *B. latecarinatus*'. In the absence of pedicellariae from this specimen it is impossible to determine if it is specifically distinct, the globiferous ones of *B. agassizi* being unusual in terminating in a slit bordered with long narrow teeth rather than a rounded opening with numerous small teeth, as in *B. latecarinatus*.

Metalia spatagus (Linnaeus, 1758)

See : H. L. Clark, 1946 : 372.
Low Is (L6) – 1.
Previous records : Torres Strait ; Low Is (H. L. Clark, 1946).

Metalia sternalis (Lamarck, 1816)

See : H. L. Clark, 1946 : 372.
Low Is : (L6) – 1 ; (L7) – 1 ; D29 – [1].

These three specimens and the single *Metalia spatagus* were all living in muddy sand.

Previous record : Low Is (H. L. Clark, 1946 ; Endean, 1957).

Class *HOLOTHURIOIDEA*

HOLOTHURIIDAE

Actinopyga ?miliaris (Quoy & Gaimard, 1833)

Bird I. (sand flat) – 1 ; Three Is (reef flat) – 1 ; Lark Passage (reef flat) – S.

The two specimens collected both have extraordinarily few spicules and their provisional identification as *A. miliaris* is mainly because of the uniformly dark colour.

Bohadschia argus Jaeger, 1833

See : H. L. Clark, 1946 : 425 (as *Holothuria argus*) ; A. M. Clark & Rowe, 1971 : 176 (as *Bohadschia argus*).
Three Is (reef flat) – 1.

Bohadschia bivittata (Mitsukuri, 1912)

See : A. M. Clark & Rowe, 1971 : 194.
Two Is (2.4) – 1.

This record provides an extension of range to Australian waters. The species has previously been recorded from southern Japan to the Philippines, Caroline Islands, Fiji, Samoa and the Bismarck Archipelago, north of New Guinea.

The single large individual was found almost buried below the surface of muddy sand. After preservation in alcohol for about a year it still shows the very distinctive colour pattern of *Bohadschia bivittata* with two broad dark brown transverse bands across the otherwise pale yellow upper side. After contraction in preservation the specimen measures 170 mm in length. The more anterior brown band is *c.* 30 mm wide but is not sharply delimited anteriorly, the area up to and around the ring of 20 tentacles being brownish. The median pale 'saddle' is *c.* 25 mm wide and the posterior brown band *c.* 40 mm wide, not sharply delimited posteriorly. The underside is uniformly pale.

H. L. Clark did not distinguish *Bohadschia* from *Holothuria*. In his key to *Holothuria* (1946 : 422) this species, with its rosettes in the body wall, runs down to section C, which includes *Bohadschia argus* marked with spots and *B. marmorata* with irregular brown blotches on the upper side.

Bohadschia marmorata Jaeger, 1833

See : H. L. Clark, 1946 : 426 (as *Holothuria marmorata*) ; A. M. Clark & Rowe, 1971 : 176 (as *Bohadschia marmorata*).
Low Is (L3) – 1 ; Two Is (2.4) – 1.

Holothuria (Acanthotrapeza) coluber Semper, 1868

See : H. L. Clark, 1946 : 428.
Three Is (reef flat) – 1.

Holothuria (Cystipus) rigida (Selenka, 1867)

See : H. L. Clark, 1946 : 432.
Two Is (reef flat) – 1.
Previous records : Murray Is ; Green I. (H. L. Clark, 1946 ; Endean, 1957).

Holothuria (Halodeima) atra Jaeger, 1833

See: H. L. Clark, 1946 : 427.
Mid Reef – S; Low Is (L3) – 3; Three Is (reef flat) – 4[2]; Three Is (3.5) – 1; Lark Passage (reef flat) – 1.

Holothuria (Lessonothuria) pardalis Selenka, 1867

See: H. L. Clark, 1946 : 437.
Three Is (reef flat) – 2.

Holothuria (Mertensiothuria) leucospilota (Brandt, 1835)

See: H. L. Clark, 1946 : 438.
Mid Reef – S; Three Is (reef flat) – 4[1].

Holothuria (Mertensiothuria) ?leucospilota (Brandt)

See: H. L. Clark, 1921 : 179.
Low Is (L5) – [1]; Three Is (3.5) – 1.

When collected these two specimens were dark brown, as usual in *H. leucospilota* but after preservation in alcohol they turned quite black, whereas the specimens positively identified as *H. leucospilota* are purplish-brown. In addition, these two were found buried on a sand flat, not on a reef flat where *H. leucospilota* is usually so conspicuous stretching out from under stones.

However, H. L. Clark (1921) notes that older individuals of this species are much more black in colour; though very contracted now, the two specimens were almost certainly distinctly larger than the rest in life. Their body walls, spicules and calcareous ring agree very well.

Holothuria (Metriatyla) scabra Jaeger, 1833

See: H. L. Clark, 1946 : 430.
Pipon Is (sand flat) – 6[1]; Bird I. (sand flat) – 3.

Holothuria (Theelothuria) sp. juv.

D32 – 1.

This small specimen has the tack-like spicules characteristic of the subgenus *Theelothuria* but cannot be identified to species.

Holothuria (Thymiosycia) arenicola Semper, 1868 (Pl. 1, fig. 4)

See: H. L. Clark, 1946 : 438.
Low Is (L4) – 5; Three Is (3.2 & 3.5) – 2; Two Is (2.2) – [1].

This species is one of the most conspicuous members of the infauna of the sand flats, burrowing to a depth of about 25 cm. One specimen harboured the commensal fish *Carapus homei* Richardson (see Mukerji, 1932; Jangoux, 1974).

Even when preserved in alcohol, these specimens show a conspicuously abrupt change in colour at about 10–20 mm from the anus, from the yellowish-brown with lines of small dark blotches, usually described for this species, to pure white, though after two years this is much less distinct than in the photograph from life shown in Plate 1. Among the 55 specimens of *H. arenicola* preserved in the British Museum collections, two show a distinctly lighter posterior end; one was collected by Gibbs in the Solomon Islands in 1965 and the other, from the 'Java Sea', was received as long ago as 1889. As far as we can ascertain, this abrupt colour change to white posteriorly has not been recorded in the literature.

Holothuria (Thymiosycia) impatiens (Forskaal, 1775)

See: H. L. Clark, 1946: 434.
Three Is (reef flat) – 2.

Labidodemas semperianum Selenka, 1867

See: H. L. Clark, 1946: 421.
Low Is (L3) – 2.
Previous records: Murray Is; Capricorn Group (H. L. Clark, 1946).

STICHOPODIDAE

Stichopus chloronotus Brandt, 1835

See: H. L. Clark, 1946: 417.
Mid Reef (reef flat) – S; Low Is (L3) – 1; Three Is (reef flat) – S; Lark Passage (reef flat) – S; Two Is (reef flat) – S.

Stichopus horrens Selenka, 1867

See: H. L. Clark, 1946: 418.
Three Is (reef flat) – 1.

Stichopus variegatus Semper, 1868

See: H. L. Clark, 1946: 418.
Three Is (reef flat) – 1; D17 – 1; K4 – 1.

CUCUMARIIDAE

Havelockia sp. juv.

D3 – 1; D21 – 1.

It is likely that this species would have been included in *Thyone* by H. L. Clark.

Pentacta australis (Ludwig, 1875)

See : H. L. Clark, 1946 : 392.
D21 – 2.

Pentacta cucumis (Semper, 1868)

See : H. L. Clark, 1946 : 393.
D7 – 1.
Previous records : Torres Strait (H. L. Clark, 1946) ; west of N Direction I. (H. L. Clark, 1932) ; Coppersmith I. (south of Whitsunday Group) (Endean, 1956).

Thyone papuensis Théel, 1886

See : H. L. Clark, 1946 : 399.
K8 – 1.

PHYLLOPHORIDAE

Afrocucumis africana (Semper, 1868)

See : H. L. Clark, 1946 : 404 (as *Discucumaria africana*) ; Endean, 1956 : 130 (as *Discucumaria africana*) ; A. M. Clark & Rowe, 1971 : 182 (as *Afrocucumis africana*).
Three Is (reef flat) – [2] Three Is (3.7) – 3 ; Noble I. (reef flat) – 1.

An additional specimen from the Three Islands reef flat lacks spicules in the body wall and cannot be positively identified.

Actinocucumis typicus Ludwig, 1874

See : H. L. Clark, 1946 : 403.
D47 – 1.

Phyllophorus (Phyllothuria) cebuensis (Semper, 1868)

See : H. L. Clark, 1946 : 409.
D48 – [1].

We are indebted to Dr F. W. E. Rowe of the Australian Museum for identifying this very small specimen.

This record provides an extension of range to Queensland waters from Western Australia, H. L. Clark (1938) having named as *P. cebuensis* a small specimen from Dongarra, near Geraldton, though expressing a little doubt. Previous records are from the Philippines (the type locality) and Indonesia.

SYNAPTIDAE

Leptosynapta latipatina H. L. Clark, 1921

See : H. L. Clark, 1946 : 454 (*Leptosynapta parvipatina* [lapsus]).
Low Is (L1) – 1.

The single specimen was found among *Mesochaetopterus* tubes in muddy sand. The species was previously known only from the incomplete holotype, taken at Friday Island, Torres Strait (H. L. Clark, 1921).

Opheodesoma grisea (Semper, 1868)

See : H. L. Clark, 1946 : 449.
Low Is (*Tripneustes* spit) – 1.

Rynkatorpa sp. nov. (to be described by F. W. E. Rowe; see p. 108)

D33 – 2 pieces [½] (very small).

Synaptula recta (Semper, 1868)

See : H. L. Clark, 1946 : 453 (as *Chondrocloea recta*) ; A. M. Clark & Rowe, 1971 : 188 (as *Synaptula recta*).
Beesley I. (sand flat) – 1.

CHIRIDOTIDAE

Chiridota rigida (Semper, 1868)

See : H. L. Clark, 1946 : 457.
Low Is : (L3) – 3 ; (L7) – [1].

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One of us (P. E. G.) would like to thank the Royal Society for the opportunity to participate in the Expedition to the Great Barrier Reef ; and also Dr D. R. Stoddart (Leader) and other Expedition members, particularly Dr R. F. McLean, Dr J. E. N. Veron and Mr L. Zell, for much assistance in the field. The skilful help of the Masters and crews of the M.V. *Calypso* (J. Lawlor) and R.V. *James Kirby* (D. Duncan) in carrying out the dredge survey, often under difficult conditions, is gratefully acknowledged.

TABLE 4

List of some associates of these echinoderms, collected simultaneously

HOST	ASSOCIATE	
CRINOIDEA		
Comantheria briareus	*Paradyte crinoidicola* (Potts)	Polychaete
	Myzostomum sp.	Myzostome
Comantheria or *Comanthus* sp.	*Myzostomum* sp.	Myzostome
Comanthina schlegeli	*Paradyte crinoidicola*	Polychaete
	Myzostomum sp.	Myzostome
Comanthus bennetti	*Paradyte crinoidicola*	Polychaete
	Galathea elegans Adams & White	Decapod

TABLE 4 (cont.)

HOST	ASSOCIATE	
Comanthus parvicirrus	*Myzostomum polycyclus* Atkins	Myzostome
	Myzostomum sp.	Myzostome
Comanthus samoanus	*Paradyte crinoidicola*	Polychaete
	Myzostomum sp.	Myzostome
	Galathea australiensis Stimpson	Decapod
Comatella stelligera	*Myzostomum* sp.	Myzostome
	Eulimid sp.	Gastropod
Comatula rotalaria	*Ophiomaza cacaotica* Lyman	Ophiuroid
Himerometra robustipinna	*Paradyte crinoidicola*	Polychaete
	Myzostomum costatum Leuckart	Myzostome
	Myzostomum crosslandi Boulenger	Myzostome
	Galathea elegans	Decapod
Colobometra perspinosa	*Paradyte crinoidicola*	Polychaete
Tropiometra afra	*Paradyte crinoidicola*	Polychaete
	Galathea elegans	Decapod
ASTEROIDEA		
Archaster typicus	*Ophiodromus* sp.	Polychaete
Pentaceraster regulus	*Hololepidella nigropunctata* (Horst)	Polychaete
OPHIUROIDEA		
Ophiarthrum elegans	*Hololepidella nigropunctata*	Polychaete
Ophiocoma dentata	*Hololepidella nigropunctata*	Polychaete
Macrophiothrix belli	*Hololepidella nigropunctata*	Polychaete
HOLOTHURIOIDEA		
Actinopyga sp.	*Gastrolepidia clavigera* Schmarda	Polychaete
Bohadschia argus	*Gastrolepidia clavigera*	Polychaete
Holothuria coluber	*Gastrolepidia clavigera*	Polychaete
Holothuria atra	*Gastrolepidia clavigera*	Polychaete
Holothuria leucospilota	*Gastrolepidia clavigera*	Polychaete
Holothuria arenicola	*Carapus homei* Richardson	Fish
Stichopus chloronotus	*Gastrolepidia clavigera*	Polychaete
Chiridota rigida	'Leptonid' sp.	Bivalve

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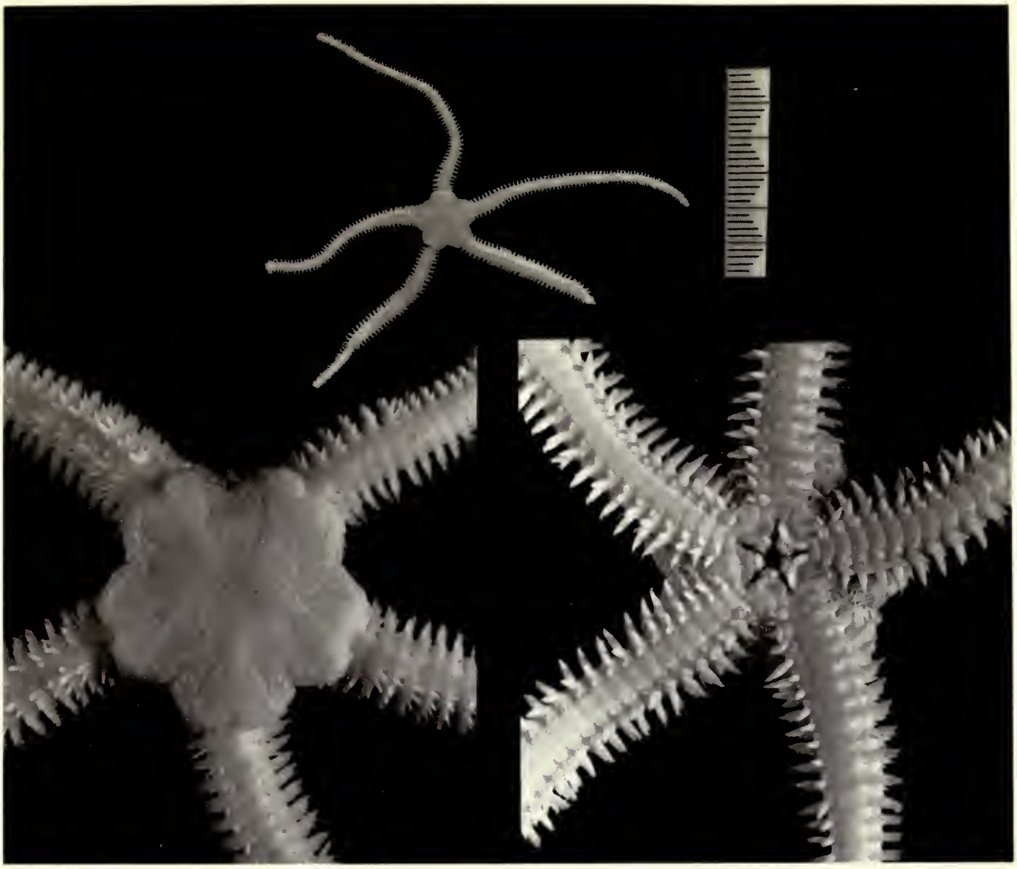
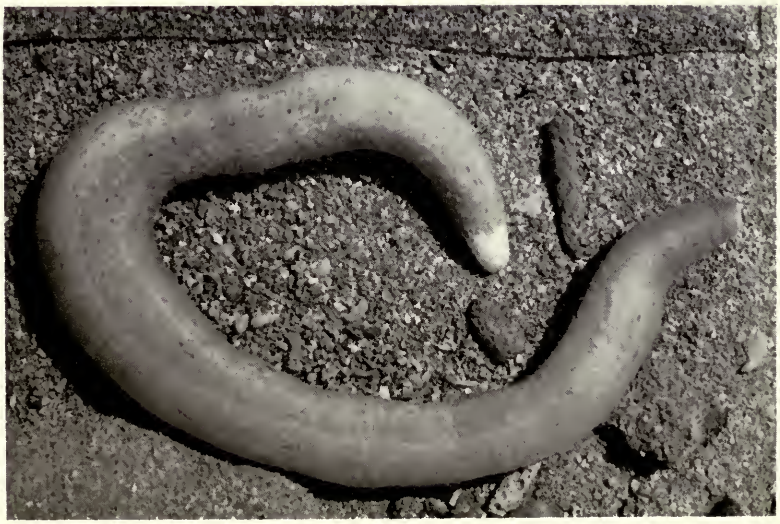
PLATE 1

Amphiura phrixocantha sp. nov. Holotype Top. Dorsal view (× 1).
Centre, left and right. Dorsal and ventral views (× 4).
Bottom. *Holothuria* (*Thymioscyia*) *arenicola* Semper, photographed in life (× ⅓).





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TILAPIINE FISHES FROM CRATER-LAKES NORTH OF LAKE MALAWI

By E. TREWAVAS

SYNOPSIS

Tilapia chungruruensis Ahl of a crater-lake in the Rungwe Mountains, about 32 km north of Lake Malawi, is redescribed from the holotype and ten of the 'cotypes' (paratypes). The population is related to the *Sarotherodon squamipinnis* group of Lake Malawi. The holotype cannot be assigned to any of the four species of this group, nor to the related species of Lakes Mweru and Rukwa, and consequently the name of neither of these can be regarded as its synonym. It may represent the result of hybridization, although this cannot be definitely assumed. Some of the 'cotypes', however, are probably *S. lidole* (Trewavas) modified by the environment.

Changes in the level of Lake Malawi may have permitted the natural populating of the crater-lake or it may have been stocked by man. All the specimens have relatively bigger heads than their Lake Malawi relatives and are sexually mature at a much smaller size. A comparison is drawn with the *Sarotherodon* species of a crater-lake in West Cameroon and with isolated populations of other species.

Lake Tschungruru is probably the same lake as that now known as Masoko. Two specimens of *S. lidole* from Lake Kingiri, a crater-lake nearer to Lake Malawi, are also described.

INTRODUCTION

THE main object of this paper is to redescribe the types of *Tilapia chungruruensis* Ahl, 1924, and to relate them to other tilapiine fishes of the genus *Sarotherodon* (formerly subgenus) to which they belong. I have also considered two specimens of this genus collected by Dr H. Albrecht in Lake Kingiri, north of Lake Malawi, and some juveniles collected in Lake Masoko by Miss C. K. Ricardo (later Dr Ricardo-Bertram) in 1937.

I have been privileged to examine the holotype and eleven of the twenty-nine 'cotypes' (paratypes) of *T. chungruruensis*, thanks to the kindness of Dr K. Deckert, who was in charge of the fish collections in the Berlin Museum at the time of the loan.

The meristic characters, the black colour and tasselled genital papilla of the males, the long pectoral fin, the long, slender caudal peduncle and the shape of the lower pharyngeal bone collectively relate these fishes to the Malawi species-flock of the *S. squamipinnis* group and distinguish them from *S. rukwaensis* and *S. macrochir*, tasselled *Sarotherodon* of neighbouring basins. At the time of Ahl's description and Ricardo's determination the four species of the Malawi group had not been distinguished. On the same morphological criteria used for the Malawi group (Trewavas, 1941 ; Lowe, 1952) I find that the holotype and two of the paratypes of *S. chungruruensis* belong to one species, not exactly identifiable with either of the Lake Malawi species, eight others to a second species which I identify with *S. lidole*. (The eleventh 'cotype' is a juvenile of 42 mm SL, too small to be determined.) I

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therefore describe them under two headings, grouping the Lake Masoko juveniles tentatively with *S. chungruruensis* and the Lake Kingiri specimens with *S. lidole*.

DESCRIPTION OF THE LOCALITIES

Ahl (1924) quoted Fülleborn's account of the Tschungruru-See. He stated that it is the Kiungvuvu of Cross, near the mission station of Neu-Wangermannshöhe. This name is not found on recent maps, but in the *Atlas* of Stuhlmann's *Deutsch Ost-Afrika* it is marked at 9°17'S, 33°50'E, north of Lake Malawi but within its drainage basin. The crater-lake Masoko lies a few kilometres NW of this at about 9°16'S, 33°43'E and is probably the same lake under another name.

Fülleborn described Lake Tschungruru as a crater-lake about 500 m in diameter and 45 m deep with no surface outlet. The water did not taste brackish.

Lake Kingiri is a crater-lake about 8 km north of Lake Malawi and 3 km north of Ipinda Ferry.

DESCRIPTION OF SPECIES

Sarotherodon chungruruensis (Ahl)

Tilapia chungruruensis Ahl, 1924 : 86.
Tilapia squamipinnis (part., nec Günther ?) ; Ricardo, 1939 : 655.

TYPE MATERIAL. Holotype : the 'type' by original designation is the largest specimen, a mature male of total length 193 mm (153+40 mm), one of thirty numbered 208 in the Zoological Museum of the Humboldt University, Berlin, collected by Professor Fülleborn about 1923 in Lake Tschungruru, a crater-lake in the Rungwe Mountains, north of Lake Malawi.

Lectoparatypes :[1] two specimens, respectively 51 and 69 mm in SL. I assign the eight other 'cotypes' examined to *S. lidole* (p. 151).

DESCRIPTION. Some of the variation is consistent with the usual allometries, so that the highest ratios for depth of body, length of snout, depth of preorbital, interorbital width and length of jaw are those of the holotype. So also is that of head-length, a less usual trend, but found also in some other phytoplankton feeders (*S. linnellii* and *S. caroli* of Lake Barombi-Mbo, Cameroons), and the length of the pectoral fin. The eye, as usual, is negatively allometric.

Proportions as % SL : depth of body 37·6–38·5 ; length of head 37·3–40·5 ; length of pectoral fin 35–42 ; length of caudal peduncle 13·8–16·0 (1·15–1·3 times its depth).

Proportions as % length of head : snout 29–38 ; eye 29·0–20·5 ; depth of preorbital 16·8–24·2 ; interorbital width 31·6–39·7 ; length of lower jaw 32, 32·8 in the small specimens, 39 in the holotype.

Teeth in 3–4 series in upper jaw, 4–5 in lower ; 42–78 in outer row of upper jaw ; with slender shafts and curved crowns, the outer bicuspid in the young, mixed bi- and tri-cuspid in the holotype, which has many of the crowns broken off; inner tricuspid, but also many of these are broken in the holotype.

---

[1] Since the holotype is not a lectotype I think that this, and not 'paralectotypes' is the correct title for those 'cotypes' that I recognize as conspecific with the holotype.

Gill-rakers on first arch 2+1+17.

Lower pharyngeal bone: see Tables 1 and 2 and Pl. 3.

Scales in 2 or 3 series on the cheek; 32 in the lateral line series, 4 or 4½ from origin of dorsal to lateral line.

Dorsal XIV 12 (holotype), XV 11 or XV 12. Anal III 10–11. Caudal truncate or very slightly emarginate, not densely scaled, but with small scales extending part-way along upper and lower rays.

Genital papilla small in young; in the holotype with several short branches arising in two groups from a club-shaped base.

Vertebrae 30 (14+16) in the holotype and one other.

Colour. The holotype, a ripening male, is dark all over, including the fins. The colour is now dark brown, probably faded from black. Even the dorsal lappets are now dark. The 69 mm specimen is pale, without markings, the vertical fins faintly dusky. In the 51 mm specimen the dorsal fin and back are dark; along the middle of the flank are four dark spots produced vertically.

ADDITIONAL SPECIMENS. Four young of 35·5–61·0 mm SL were collected in crater-lake Masoko in 1937 by Miss C. K. Ricardo (later Dr Ricardo-Bertram). These also belong to the *S. squamipinnis* group and both jaws and pharynx are too well toothed for *S. lidole*. There are 32 or 33 scales in the lateral line series, 8 or 9 soft rays in the anal fin, 17 or 18 gill-rakers on the lower part of the first arch. The dorsal formula is XV 10 (f.1), XV 11 (f.2) or XVI 10 (f.1). The three of 56–61 mm have 4–5 rows of teeth in the upper jaw, 5–6 in the lower; the length of head is 36% SL. There are 6 dark vertical bars on the body, accentuated above the lateral line.

We have not so far succeeded in distinguishing between the four Malawi species at such a small size and in placing these in *S. chungruruensis*. I am merely indicating that like the types they are not *S. lidole* and may be one of the other species or the result of hybridization between some of them.

Sarotherodon lidole (Trewavas)

Tilapia lidole Trewavas, 1941 : 297; Bertram, Borley & Trewavas, 1942 : 34, fig. 4C & D; fig. 6C; Lowe, 1952 : 2–65.

DESCRIPTION (of eight specimens from Lake Tschungruru and, in brackets, two from Lake Kingiri).

The Tschungruru specimens are eight of the paratypes of *T. chungruruensis*, nos 2 and 4–10 in Table 1. The two Kingiri fishes measure 139+31·5 and 162+39 mm to the end of the middle caudal rays; they are listed at the end of Table 1.

Proportions as % SL: depth of body 34·8–40·0 (40·5, 38·4); length of head 39·4–42·4 (38·5, 38·6); length of pectoral fin 38·0–43·3 (41·5, 40·0); length of caudal peduncle 15·3–16·8 (16·3, 15·7); length of lower jaw 11·6–14·8.

Depth of caudal peduncle contained 1·27–1·5 times in its length.

Proportions as % length of head: length of snout 34·2–39·0 (32·6, 26·8); diameter of eye 21·3–24·4 (24·2, 21·0) with no evidence of allometry; depth of preorbital 18·7–23·8 (22·4); interorbital width 34·0–44·5 (45·2, 44·7); length of lower jaw 27·8–39·6 (31·8–32·3).

Proportions of lower pharyngeal bone: see Tables 1 and 2. Pharyngeal teeth very fine, in a restricted area.

Teeth in 3 rows in both jaws with an incomplete fourth in a few; with long, slender shafts and expanded crowns; those of outer row bicuspid in small specimens, in some bigger fishes with an admixture of tricuspid and occasionally a few unicuspid, often but not always by wear; a few posterior often simple. Teeth of inner rows tricuspid unless with worn crowns. Number of outer teeth in upper jaw 52 at SL 65·5 mm, 70–82 from 86 to 162 mm.

Gill-rakers 2–4+1+17–20 on first arch.

Scales on cheek in 2–3 rows, occasionally a few small scales of a fourth row; lateral line series 33–34; 4, 4½ or 5 from origin of dorsal fin to lateral line, about 20 around caudal peduncle.

Dorsal XIV–XV 10–11 (XVI 11, XVII 10 in Lake Kingiri); anal III 8–10.

Vertebrae 31 in three counted.

Genital papilla of a male of SL 143 mm large, with two groups of short papillae at its distal end, the pore between them. A female of SL 123 mm has enlarged ovaries, in which the biggest egg is 3 mm in long diameter.

TABLE 1

Data from the holotype and ten paratypes of *Sarotherodon chungruruensis* (Ahl) in order of size

No. of specimen	SL (mm)	Head % SL	Ph.l. % head	Ph.w. % head	Ph.l/w	Ph.bl./dent.	Rows teeth in lower jaw
1·	**51**	**37·3**	**31·6**	**31·6**	**1·0**	**1·3**	**4–5**
2.	65·5	40·7	36·3	26·2	1·4	1·8	3
3·	**69·0**	**37·7**	**34·6**	**32·7**	**1·06**	**1·2**	**4**
4.	86·0	42·0	36·4	27·8	1·3	2·5	3
5.	93·5	40·6	37·0	26·3	1·4	2·06	3
6.	123·0	39·4	37·5	26·0	1·4	3·4	3
7.	125·0	42·4	39·6	27·0	1·47	3·88	3
8.	126·0	40·8	34·0	25·6	1·32	3·4	3
9.	141·0	40·4	38·0	25·0	1·5	3·0	3–4
10.	143·0	39·6	40·7	28·6	1·42	2·7	3
11.	**154·0**	**42·5**	**35·5**	**28·6**	**1·24**	**1·4**	**4–5**
LAKE KINGIRI							
	139·0	38·5	37·6	27·2	1·38	1·88	3
	162·0	38·6	36·0	26·2	1·37	2·2	3

No. 11 is the holotype and nos 1 and 3 resemble it in the proportions of the lower pharyngeal bone and number of rows of teeth in the jaws; data for these are in bold type. The other specimens are determined as *S. lidole*. The measurements of the lower pharyngeal bone are its median length (Ph.l.), greatest width (Ph.w.), both expressed as % length of head; the median length divided by the width (Ph.l/w.) and the length of the anterior blade divided by the median length of the dentigerous area (Ph.bl./dent.). For comparison the same data are given for two specimens of *T. lidole* from Lake Kingiri.

TABLE 2

Summary of Table 1

	S. chungruruensis holotype and lectoparatypes (Specimens 11, 1 and 3)	Other 'cotypes', determined as *S. lidole* (Specimens 2, 4–10)	Two *S. lidole* from Lake Kingiri
Ph.l. % head	31·6–35·5	34·0–40·7	36·0, 37·6
Ph.w. % head	28·6–32·7	25·6–28·6	26·2, 27·2
Ph.l./w.	1·0–1·24	1·3–1·5	1·37, 1·38
Ph.l./dent.	2·2–2·4	2·8–4·8	2·8, 3·2

TABLE 3

Pharyngeal proportions in Lake Malawi

	S. lidole	*S. squamipinnis* and *S. saka*	*S. karongae*
N	12	5	4
SL (mm)	230–285	200–250	150–235
Phar.l./w.	1·33–1·47	1·22–1·38	1·29–1·35
Phar.l./l.dent.	3·0–4·5	2·4–3·1	2·16–2·25

Colour. Small specimens and females with five dark blotches, vertically drawn out, along the side and some with two fainter on the caudal peduncle; vaguer markings in a more dorsal row; one male almost uniformly dark. Males with broad dark margin on dorsal fin and dark anal fin, in one with narrow white margin (as preserved). Females with no marginal dorsal band. Smaller specimens with a tilapia-mark.

Caudal clear in small specimens; in mature males of Lake Tschungruru dark or dusky with a white margin or upper corner. Male of Lake Kingiri with caudal dark proximally, distally with a dark reticulum and a pale margin.

COMPARISON WITH SPECIES OF LAKE MALAWI

S. lidole

1. *Resemblances*

I have identified eight Tschungruru specimens with this species because of the proportions of the pharyngeal, the narrow bands of teeth in the jaws and the general shape.

(a) Pharyngeal. In adults of Lake Malawi, all bigger than the crater-lake specimens, the median length of the pharyngeal bone is 1·38–1·5 times its greatest width. In the crater-lake the ratio is 1·3–1·5 (Tables 1 and 2), including specimens down to 65·5 mm SL, thus smaller than the sizes at which the species has been recognized in Lake Malawi. The dentigerous area is restricted and the blade is long, also characters distinguishing *S. lidole.*

(b) Jaw teeth. The inner teeth of the jaws are set in irregular rows and the formula '3–4', including the outer row, expresses this irregularity rather than variation within the size-range of the crater-lake sample. In Lake Malawi, even in the much bigger adults, 3–5 is the range, in contrast to 4–7 in *S. saka, S. squamipinnis* and *S. karongae.*

(c) Plates 1 and 2 show the characteristic position of the greatest depth of body in front of the dorsal fin in contrast to the other species.

2. *Differences from the Malawi population*

(a) Length of head. *S. lidole* in Lake Malawi is credited by the fishermen with a big head and the ratio there shows a higher range, though with a wide overlap, in comparison with that of the other species. It is 34·0–38·5% SL in Lake Malawi in contrast to 39·4–42·4 in the crater-lake. It is true that the Malawi specimens are bigger, but smaller Malawi fishes of indeterminate species, probably including *S. lidole*, have head ratios in the lower part of the range. The biggest ratios are found in much bigger, mature fishes. The significance of this will be discussed below.

(b) Size at sexual maturity. Lowe (1952 : 24) gives the minimum size at sexual maturity for both males and females of *S. lidole* as 28 cm TL (about 240 mm SL). In contrast, the crater-lake male of SL 143 mm (TL about 17·5 cm) already has an enlarged genital papilla terminating in a short tassel, and a female of SL 123 mm (TL 15 cm) has an ovarian egg of 3 mm long diameter.

The small size and early age of sexual maturity in pond populations of other species of *Sarotherodon* are well known (Lowe, 1955 : 365 ; 1958 ; Hickling, 1962, 1963).

In the other crater-lake, Kingiri, the two available specimens have a head ratio at the upper end of the Malawi range. Their gonads were removed, but a short tassel on the papilla of the male shows that here too sexual maturity occurs at a smaller size than in the Great Lake.

S. chungruruensis

The holotype contrasts with the *S. lidole* of the same crater-lake in the shape of the pharyngeal bone as expressed in its length : width ratio as well as the bigger dentigerous area relative to the length of blade (Pl. 3 and Table 2). It also has more rows of teeth in the jaws and that this is not only because of its greater size is confirmed by the small lectoparatypes, which also combine a wider tooth-band with a general shape contrasting with that of *S. lidole* (Pls 1 and 2).

The pharyngeal bone of the holotype contrasts more with that of the *S. lidole* of Lake Tschungruru than with those of Lake Malawi as figured by Bertram *et al.* (1942, fig. 6C). Column B of that figure, labelled *T. squamipinnis*, includes pharyngeals also from *S. saka* (Lowe) (at that time not recognized as distinct), but from what we now know of *S. saka* these would be the pharyngeals with the broadest dentigerous area, and those with a concave-sided dentigerous area would be *S. squamipinnis*. It is the latter that most resemble the pharyngeals of *S. chungruruensis*, but the breeding male of *S. squamipinnis* is pale blue with a white head, that of *S. saka* black, as *S. chungruruensis* must have been.

The character of the pharyngeal bone may well have changed in the environment of the crater-lake, so this is not a final argument for not identifying *S. chungruruensis* with *S. saka*. The holotype (and indeed some of the others) may have been the result of hybridization between, for example, *S. saka* and *S. lidole*.

SIGNIFICANCE OF THE BIG HEAD

Not only is there a high head : body ratio in the *S. lidole* of the crater-lake, but the same ratio in the type and lectoparatypes of *T. chungruruensis* is in the highest part of the range for all the species of this group in Lake Malawi.

Big heads have been found in small populations of other species of *Sarotherodon*. Two lagoon populations of the type species, *S. melanotheron*, have head ratios ranging higher than the range for the rest of this widespread species. The type specimens of *S. niloticus eduardianus* occupied a small crater-lake on the lower slopes of Ruwenzori, near enough to the shore of Lake George to have received its fish population from that lake during an exceptionally wet season. They had evidently become more crowded as time went on and when caught were stranded on the shore of the shrinking lake. Their head-ratios ranged from 36·6 to 39·8% SL, nearly all greater than in the parent population. The *S. niloticus* in Buhuku Lagoon when it was temporarily isolated from Lake Albert (see Lowe, 1958) had head-lengths ranging from 36·4 to 41·0% SL in contrast to 34·3 to 39·6% in a sample of comparable size from the open lake. The *S. niloticus vulcani* of Crater-lake A on the central island of Lake Rudolf provide a further example. Most of the endemic cichlid species of the Cameroons crater-lake, Barombi Mbo, are characterized by big heads, and *S. linnellii* and *S. caroli* provide an interesting parallel to *S. lidole* and the rest of the Malawi species-flock, both structurally and ecologically (Trewavas *et al.*, 1972).

The relative growth phenomenon resulting in a big head is known in pisciculture in the 'hunger-form' of the common carp.

THE ORIGIN OF THE TSCHUNGRURU (?=MASOKO) FISH POPULATION

Dixey (1926) gives the evidence for previous surface levels of Lake Malawi. The level has been falling since the Tertiary, for which epoch two levels have been determined, respectively 300 m and 210 m above the present level. The fall is attributed mainly to subsidence of the rift floor. The Tertiary lake consisted only of the northern part, which extended from about 32 km to the north-west of the present northern end to about the latitude of Deep Bay (10°24′S). During the Quaternary the lake extended southwards and when it was 120 m above its present level still included an area 80 km north of the present north end.

Just where the limit was at the time, relatively recent, of the volcanic activity that produced the Rungwe Mountains, including the Masoko crater, is not certain, but it seems quite possible that it was near enough to be supplied naturally with its fish fauna from Lake Malawi or one of its affluent rivers.

If it was stocked by man the source would be the same, namely the fry that abound among the grasses and reeds of the banks ; they might have survived a journey of at the most 30 km in a calabash or a cool clay pot.

Lowe (1952, 1953) has described the breeding places, seasons and colours that characterize the three tasselled tilapias of the Malawi flock at the south end of the lake. Her stay of one month (March) at Karonga near the north end was not long enough to establish such distinctions, and she found there some specimens that seemed 'equivalent to *T. squamipinnis* and *T. saka* at the south end of the lake', that is to a single representative of these two species, as well as some that could be assigned to each of them. The northern species, *S. karongae,* was also present and there was evidence that *S. lidole* was caught at a different time of the year (October).

None of the examined types of *S. chungruruensis* has a pharyngeal bone big enough for *S. karongae* so that the source-species must be *S. lidole* and one or both of the other two.

The seasons and topography in the north of Malawi do not provide the same framework as that within which the three southern forms preserve their identity. Still more is this true of Lake Masoko and although *S. lidole* has kept its characteristics with but slight modification, I find it impossible to be sure that *S. chungruruensis* is identical with either *S. squamipinnis* or *S. saka,* or to justify the synonymizing of its name with either the older *S. squamipinnis* or the junior *S. saka.* It seems more expedient to retain the name *chungruruensis* for the section of the crater-lake population that may be a hybrid between two or more of the southern species or a modified population of *S. saka,* and to refrain from suppressing the latter name in favour of that of such a doubtful form.

A fresh examination of the Lake Masoko population and its ecology with these possibilities in mind would be interesting. The specimens collected by Ricardo in 1937 are too young to provide evidence, but they do show that fish were still in the lake at that time.

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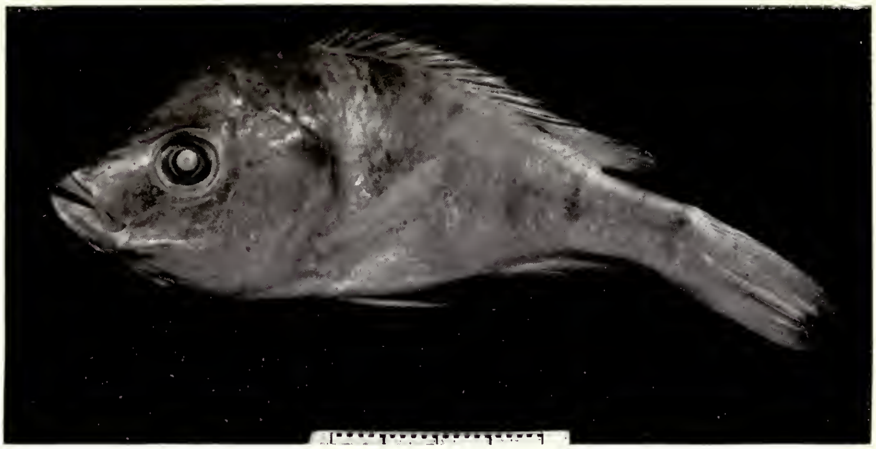
PLATE 1

Above, *Sarotherodon lidole* of SL 125 mm from Lake Tschungruru. Below, *S. chungruruensis*, holotype.



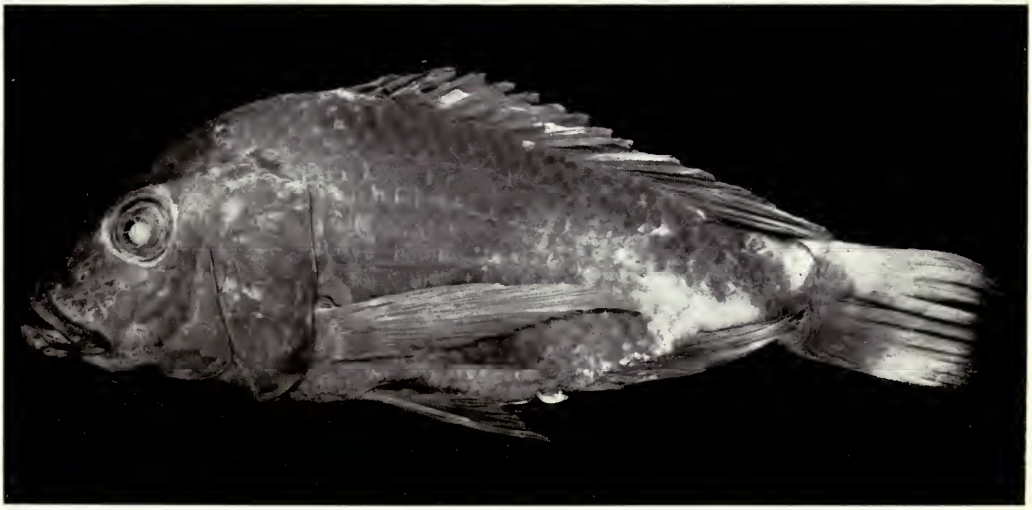


PLATE 2

Above, *S. lidole* of SL 65·5 mm from Lake Tschungruru. Below, *S. chungruruensis*, a lecto-paratype of SL 69 mm.

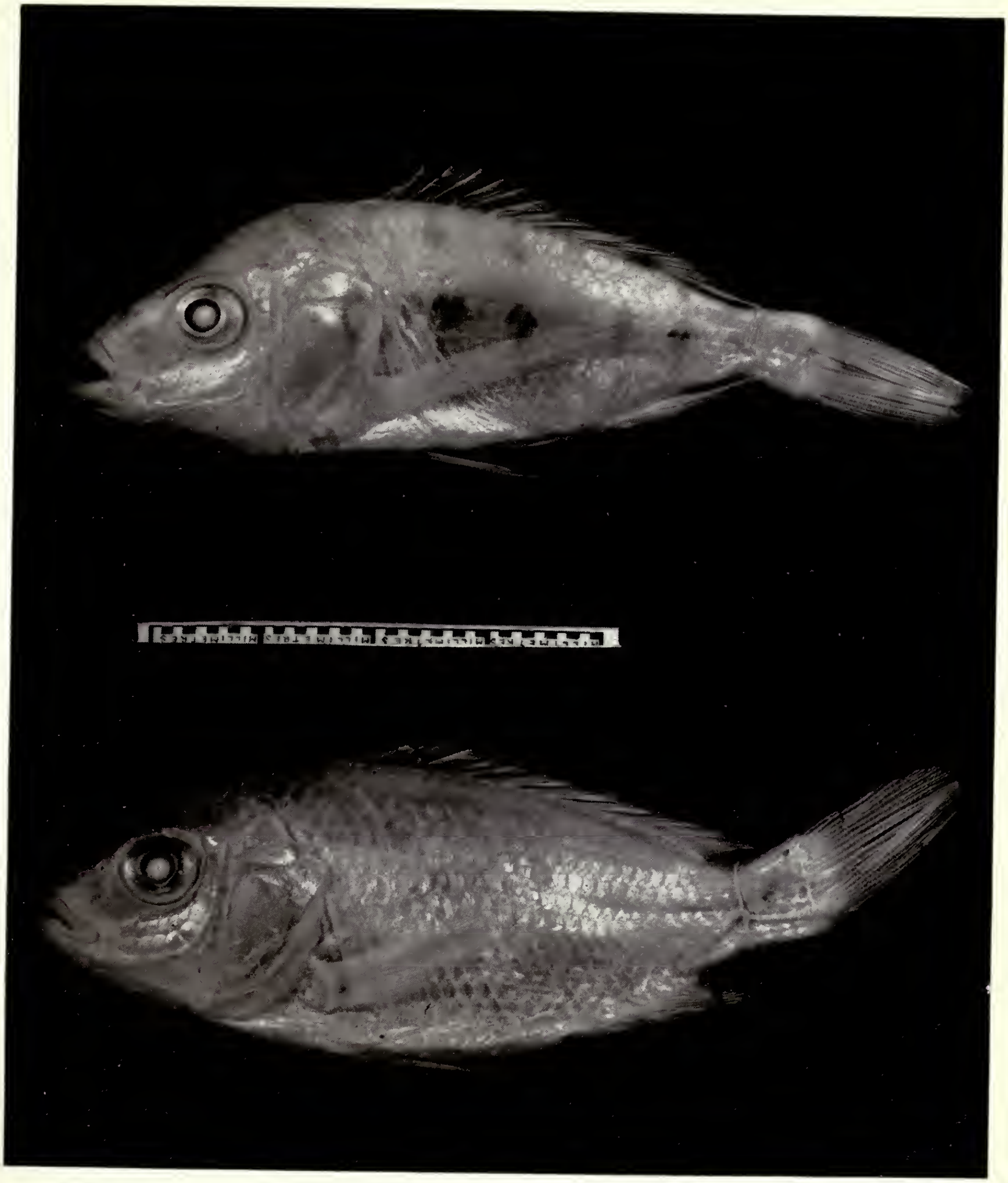
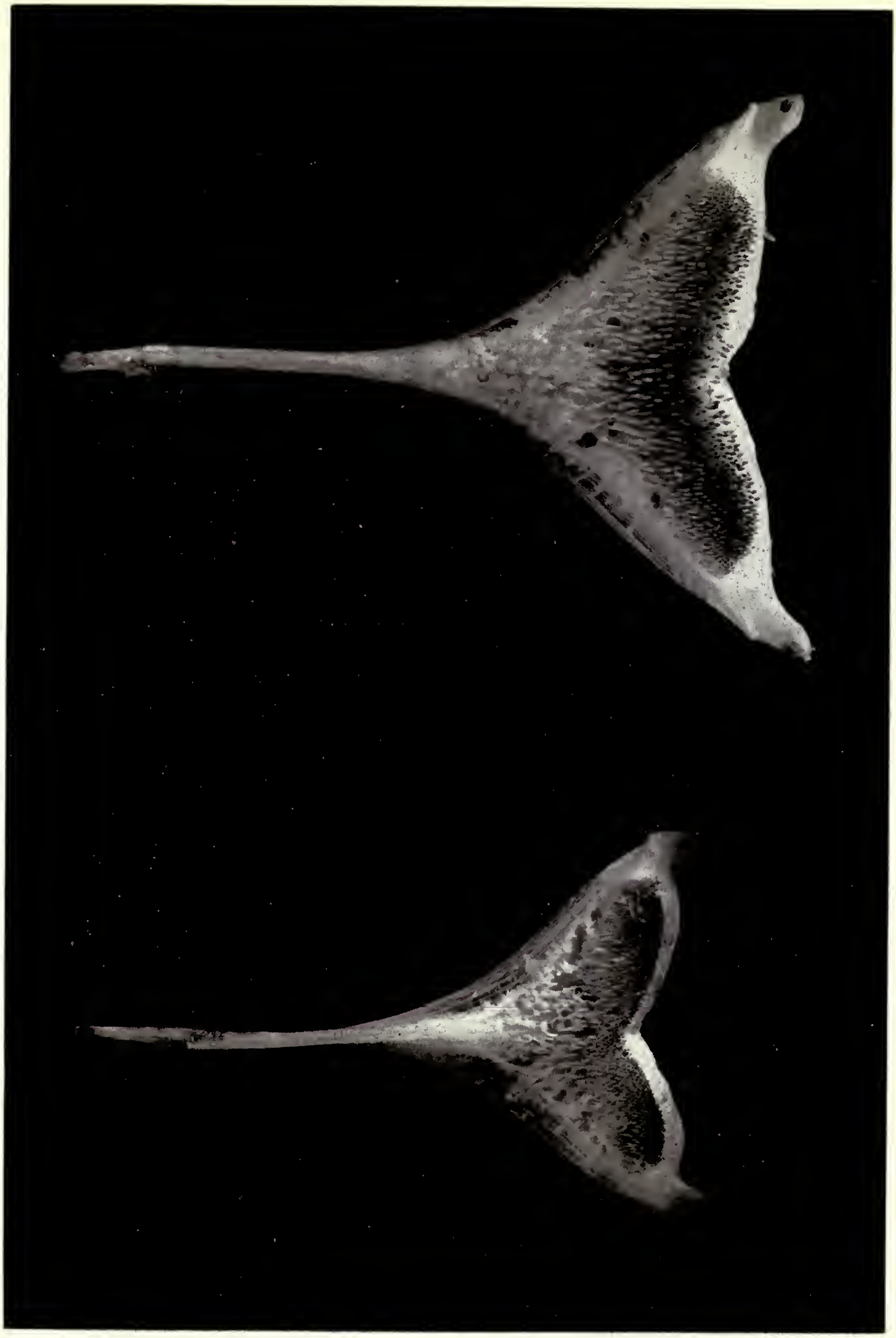


PLATE 3

Lower pharyngeal bones of, above, the holotype of S. *chungruruensis* ; below, a specimen of S. *lidole* of SL 125 mm from Lake Tschungruru. (× 8·25).



A NEW SPECIES OF *HEMICHROMIS* (PISCES, CICHLIDAE) OF SIERRA LEONE AND LIBERIA

By A. I. PAYNE AND E. TREWAVAS

INTRODUCTION

WHILE the junior author (A. I. P.) was making a general survey of the freshwater fishes of Sierra Leone, he found a hitherto undescribed species of *Hemichromis*. Some specimens were taken in baited plexiglass traps similar to that described by Breder (1960) as a fry-trap ; others were caught by hook and line.

Among earlier collections from Sierra Leone in the British Museum (Natural History) we found that those of Mr N. W. Thomas, received in 1915, and Mr T. S. Jones, agricultural officer in the territory in the 1950s, also contained examples of the new species. The juveniles from Mr Jones had been found sufficiently striking to have been labelled with a query as to species. Two from Liberia presented by Mr E. Roloff in 1972 and provisionally labelled '*Hemichromis* sp.' also belong to the new species.

The description below is based mainly on preserved material, but the colour is described from life.

DESCRIPTION OF NEW SPECIES

Hemichromis fugax sp. n.

HOLOTYPE. ♂, 72+19 mm, from a forest stream, Kassewe Forest Reserve, Sierra Leone.

PARATYPES. Five specimens, 41–76 mm in SL from Kassewe, the Gbangbar system near Moyamba and from a small stream with muddy bottom near Njala, as listed on p. 166.

DESCRIPTION. Details of these specimens (except the smallest), two from Victoria, Sierra Leone, and one from a stream about 50 km from Monrovia, Liberia (coll. Roloff), are given in Table 1. The 41 mm paratype, having been preserved with the mouth thrust forward, is unsuitable for measurement of proportions.

Upper profile of head straight, lower jaw slightly projecting.

Cheek with 3 or 4 horizontal rows of scales, in some 1 or 2 small scales in addition.

Teeth of jaws unicuspid, in one row in lower jaw (rarely 1 or 2 inner teeth), one and a short second row in upper jaw, the lengths grading smoothly from longer anterior to shorter posterior.

Gill-rakers short, 2+1+5–7 on the first arch, the 1 or 2 lowest often abruptly smaller than the others.

Bull. Br. Mus. nat. Hist. (Zool.) **30**, 5 *Issued* 28 *October* 1976

TABLE 1

Proportions and some meristic characters in *H. fugax*

	Holotype	Paratypes						
	Kassewe	Kassewe		Moyamba	Njala	Victoria		Liberia
SL (mm)	72	76·5	66·5	70	43	80	53·5	59
As % SL								
Depth	36·1	34·6	34·6	35·7	34·8	34·4	34·6	35·6
Head	36·8	38·5	39·8	39·3	38·8	38·2	39·8	39·2
sn	11·5	11·8	12·9	12·2	10·5	12·1	13·1	12·0
int	9·15	9·3	9·8	9·45	8·6	9·25	9·35	8·5
l.j.	15·3	15·9	15·8	16·5	17·0	15·3	16·8	16·1
c.p.l.	13·9	14·4	13·5	11·7	11·9	12·5	14·0	12·9
c.p.d.	16·8	15·7	15·0	16·8	16·6	16·4	16·8	16·3
P	24·6	25·5	22·6	25·0	26·0	23·7	25·6	24·6
As % head								
sn	31·8	30·6	32·5	31·0	27·0	31·7	32·8	30·2
eye	26·8	22·0	23·0	22·5	28·8	22·8	26·3	28·1
pr	11·5	15·9	15·1	12·7	12·0	16·35	15·5	11·7
int	25·3	24·0	24·5	24·0	22·0	24·0	23·5	21·3
u.j.	34·8	33·9	34·0	33·0	30·6	32·7	35·2	31·1
l.j.	42·5	41·4	39·7	41·8	43·7	39·9	42·2	39·4
Sc.l.l.	26	27	26 ?	26	25	26	—	27
Sc.D-l.l.	3½	3½	3	3½	3½	4	4	4
D	XIV 11	XIV 12	XIV 11	XIV 11	XIV 11	XIII 12	XIII 12	XIV 11
A (III+)	8	9	8	8	8	8	8	8

Head = length of head ; sn = snout, from middle of upper lip to edge of orbit ; pr = depth of preorbital bone ; int = interorbital width, the roof of the skull between the eyes ; u.j. = upper jaw, from middle of upper lip to end of maxillary ; l.j = lower jaw, from middle of lower lip to end of retroarticular ; c.p.l. and c.p.d. = length and depth of caudal peduncle ; P = length of pectoral fin ; Sc.l.l. = no. of scales in lateral line series, resuming at the end of the upper lateral line with the lower lateral line scale (pierced or not) in the oblique row behind, the row used sloping downwards and forwards ; D = dorsal fin-rays ; A = soft anal rays. SL = Standard Length.

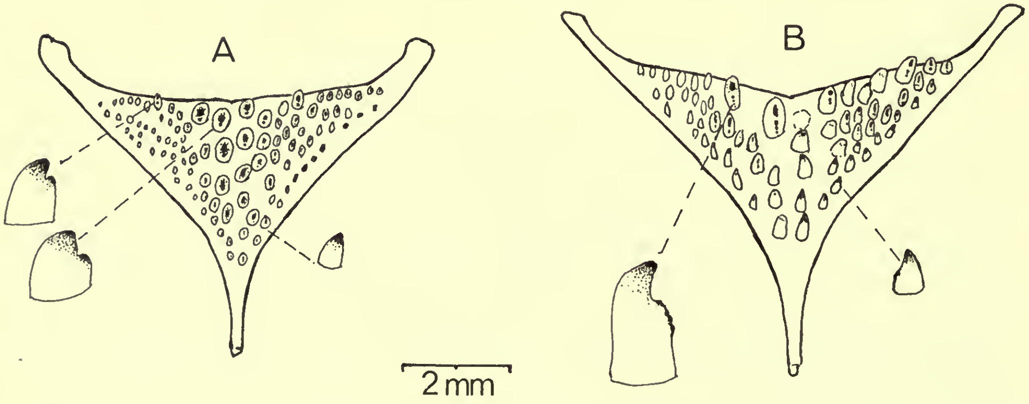


FIG. 1. The lower pharyngeal bones of *H. bimaculatus* (left) and *H. fugax* (right).

Scales cycloid with gothic circuli, 25 to 27 in the lateral line series, 3, 3½ or 4 from origin of dorsal to lateral line.

Caudal fin rounded. Length of caudal peduncle 0·75–0·9 of its depth.

Lower pharyngeal bone hastate (Fig. 1) with rather long lateral apophyses. Teeth slender, but the posterior ones of the middle rows may be worn down ; lateral posterior and several others with a crest of 1–4 small brown points in front of the main cusp. In the Liberian specimen some teeth with crest not divided into points, others with one, two or three in addition to the main cusp ; anterior teeth unicuspid. Teeth of posterior row 16–20.

Colour in life (taken straight from the water). General appearance olive brown with three approximately equidistant black blotches on each side, the first on operculum, the third at base of caudal ; much red on the fins.

Head with variable gold and red streaks on cheek and gill-cover and a greenish gold rim to the opercular spot. A circumpupillar gold ring, rest of iris grey or (in two of four observed) with red lower quadrant. Lips and chin sometimes tinged red. Lappets of dorsal fin, apex of soft fin and often also its upper edge bright red ; a clear submarginal band ; rest of fin membrane golden-yellow to pinkish with clear or pale blue spots. Anal fin clear proximally, reddish distally. Caudal fin with distal quarter to three-quarters bright red, proximally yellowish ; a clear submarginal streak underlining the red upper corner. Pectoral transparent, colourless or yellow. Pelvics clear with red or black leading edge.

After a minute or two out of water small pale turquoise spots may appear on the flank, but these are much smaller and less iridescent than those of *H. bimaculatus* Gill. With time reddish centres to the scales may also appear.

After two days in a tank one fish became much more sombre and the middle flank spot disappeared. A dark bar through the eye became pronounced and eight faint vertical bars could be switched on.

Preserved specimens show the three lateral blotches and often traces of the vertical bars.

DIAGNOSTIC FEATURES. Distinguished from *H. bimaculatus* by the long, acute snout and narrow interorbital space, giving the ratio of Table 2 (p. 164) and from *H. fasciatus* by lower numbers of scales (29–30 in *H. fasciatus*) and the fact that the anterior teeth are not abruptly contrasted in length with the rest but grade smoothly into the series.

ECOLOGY. The fish has been caught in fairly fast-flowing forest streams, where it tends to lie in the lee of weed-beds, stones or logs, and also in swampy areas. In five localities sampled it was accompanied by *H. thomasi* (Boulenger) (three places) or *H. fasciatus* Peters (two places), but not by *H. bimaculatus*. Although both species were sent by N. W. Thomas in 1915 from 'Victoria' we have no details of the locality or localities in which they were taken.

DISTRIBUTION. The sites where *H. fugax* has been found in Sierra Leone, along with the records for *H. bimaculatus*, are indicated in Fig. 3. *H. fugax* appears to be restricted to the river systems east of the Rokel and the Freetown Peninsula. Samples from the most easterly rivers of Sierra Leone, Moa and Mano, have not yet been obtained, but some juveniles described below were taken not far west of River Moa and no doubt it will be found in suitable places between here and the Liberian locality.

H. bimaculatus also occurs in the east of Sierra Leone but in the territory so far it has been located only in the physiologically more demanding brackish water areas of Sherbro Island and the coastal region opposite, including Lake Kwarko, a lagoon in the waterways parallel to the coast into which Rivers Waanje and Sewa drain. *H. bimaculatus* may therefore be physiologically more adaptable than *H. fugax*. It is widespread in other African territories.

The Liberian specimen of *H. fugax* mentioned above and a smaller one collected by Herr Roloff at the same time show that the range of *H. fugax* must extend eastwards, but the limits have yet to be determined. We have not found it among the material from the rest of Africa in the BMNH.

JUVENILES OF THE SPECIES OF *HEMICHROMIS*

Young *H. fugax* of about 15 mm SL obtained at Kassewe have a black median longitudinal stripe from the operculum to the end of the caudal peduncle, in preserved specimens ending in a slightly darker blotch at the base of the caudal fin.

Seven young of 21·0–22·5 mm SL from Potoru (a few kilometres west of the expanded part of River Moa), preserved in the BMNH, show this broad band expanded at the position of the mid-lateral blotch. At the base of the caudal fin it ends as an intense black blotch, narrowly extended on the middle caudal rays to the tip of the fin (Fig. 2). These have the acute snout and triradiate pharyngeal bone characteristic of *H. fugax*, in contrast to young of *H. bimaculatus* of the same size.

Young of *H. bimaculatus* from Bonthe, Sherbro Island (where adults have also been collected), show in contrast separate opercular, mid-lateral and caudal blotches with no extension on to the caudal rays (Fig. 2). They have the more robust pharyngeal bone characteristic of this species. In Lake Kwarko (or Kwako) the young are similar.

The difference in the pigmentation of the caudal between the two samples of *H. fugax* suggests that this pattern may not be strictly specific ; or possibly the fact that those lacking the caudal streak were smaller may be significant. In *H. bimaculatus* too there is some variation. In a sample of thirteen, 15·5–44·5 mm in SL, from Kiyawa River near Katagum, Nigeria, the two smallest have the caudal blotch produced a short distance on the caudal fin and between the mid-lateral and caudal blotches is a dusky band. The same is true of a 20·5 mm juvenile from about 19 km north of Monrovia taken with two adult *H. bimaculatus*. It has the appearance of *H. bimaculatus*, but the pharyngeal bone is equivocal. (This sample suggests that a borderline between the distribution of *H. fugax* and *H. bimaculatus* may lie between 20 and 50 km from Monrovia.)

Some fry of *H. fasciatus* from Sherbro Island have the lateral band emphasized at the positions of the future lateral blotches and continued on the middle caudal rays. This caudal extension was not figured for young of this species at Yangambi,

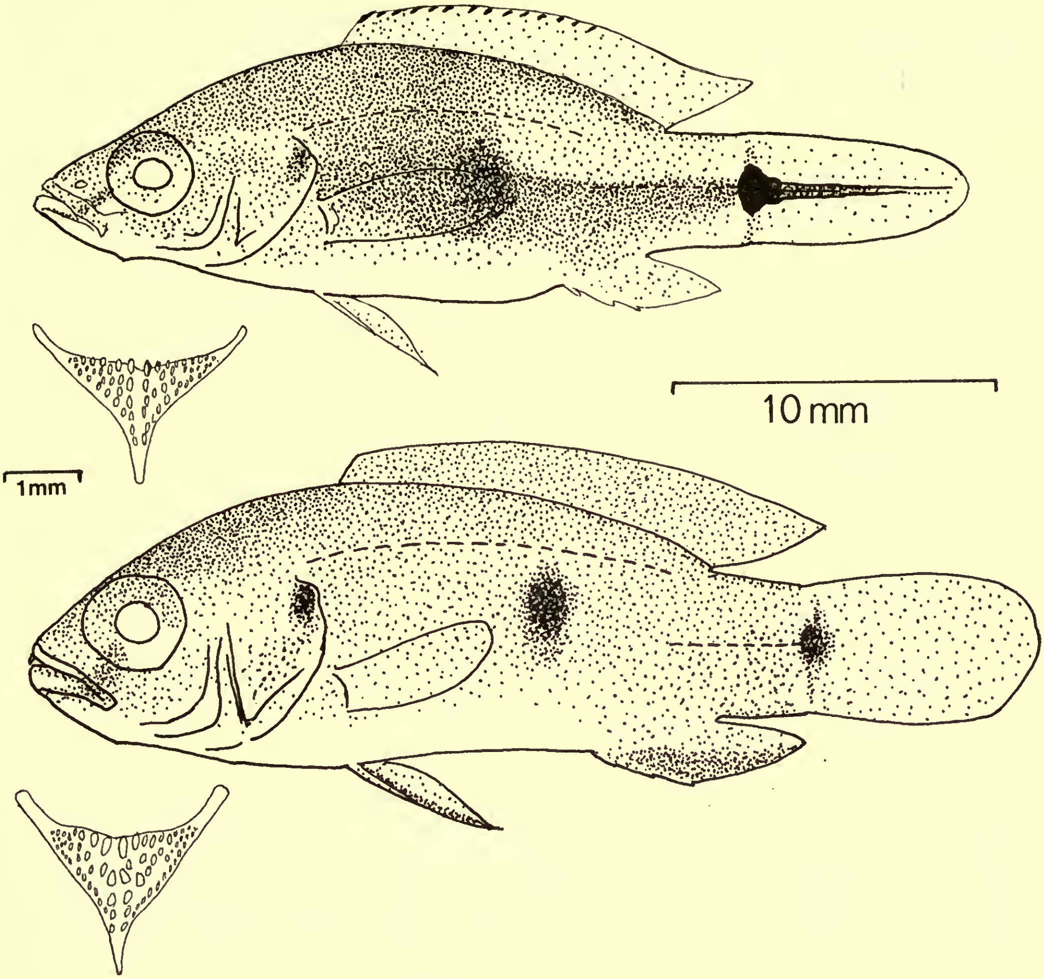


Fig. 2. Juveniles of (above) *H. fugax* from Potoru and (below) *H. bimaculatus* from Bonthe with their pharyngeal bones.

Congo, by Gosse (1963, fig. 17), but the two 'forms', A and B, of *H. fasciatus* are found in Sierra Leone and the fry may give a clue to their distribution there.

A recent account of the breeding and rearing of young of *H. fasciatus* from Liberia (Nieuwenhuizen, 1975) shows, among other handsome photographs, a shoal of 3-week-old fry. Their colour-pattern is almost exactly that of our fry from Potoru (Fig. 2), but with a more pronounced upper stripe on each side of the base of the dorsal fin. The identity of our juveniles with *H. fugax* has been confirmed by the meristic characters (scales in lateral line series 26–27, against 29–30 in *H. fasciatus*, both 'forms') and that of Nieuwenhuizen's fry by the photograph of the parent, which has five black blotches along the side behind the opercular spot.

This is probably the 'B form' of *H. fasciatus* (? =*H. elongatus* Guichenot in Duméril, 1859 cf. Loiselle, quoted in Trewavas, 1974) since the 'A form' is notoriously so aggressive that it is almost impossible to rear it in an aquarium.

RELATIONSHIPS OF *H. FUGAX*

In meristic characters this species cannot be distinguished from *H. bimaculatus* Gill, also abundant in Sierra Leone, but it is easily recognized by the different colouring, especially the lack (or lower brilliance) of the turquoise spots on the flanks, and by the acute snout (Pl. 1 and Fig. 2). The difference in snout length between the two species (Table 2 and Fig. 3) is slight, with some overlap, but the interorbital width is less in *H. fugax* and the snout/interorbital ratio consequently gives a reliable difference between the two species. They are also distinguished by the pharyngeal teeth, fewer and more slender in *H. fugax*, sometimes with up to four minor cusps, whereas in *H. bimaculatus* some of the median teeth are stout and blunt. In both adult and juvenile the pharyngeal bone is more robust in *H. bimaculatus*. The teeth of the jaws are variable in both species, an inner series being present or absent, when present of a few teeth only. In neither species are the anterior so sharply contrasted in size with the others as in *H. fasciatus* Peters, but the shape of the snout and mouth in *H. fugax* approaches that in *H. fasciatus*.

TABLE 2

Length of snout (Sn) and interorbital width (Int) in *Hemichromis fugax* and *H. bimaculatus* and the ratio of snout to interorbital width

	H. fugax (N = 13)		*H. bimaculatus* (N = 19)	
	Range	Mean	Range	Mean
SL (mm)	40·7 –80·5	61·21	44·0 –100·0	61·45
Sn (% head)	26·0 –30·6	28·33	22·6 – 28·6	25·55
(% SL)	9·5 –11·9	10·88	8·45– 10·2	9·27
Int (% head)	20·0 –23·0	21·20	22·2 – 26·8	24·73
(% SL)	7·6 – 8·95	8·18	8·2 – 9·85	8·96
Sn/Int	1·23– 1·50	1·33	0·86– 1·19	1·04

The significance of the difference in colour-pattern between our samples of juveniles can only be judged after tests of variation between populations and developmental stages. Possibly the juvenile pattern is another feature in which *H. fugax* resembles *H. fasciatus* and differs from *H. bimaculatus*.

We have mentioned *H. thomasi* as though it were a species of *Hemichromis*, as Loiselle & Welcomme have treated it (1972). This is, in any case, an isolated species not liable to be confused with any of the currently recognized species of *Hemichromis* and certainly not with *H. fugax*, having a very short, blunt snout and smaller, more numerous pharyngeal teeth.

We have also examined syntypes (or topotypes) of *H. letourneuxi* Sauvage (1880a) from Lake Mareotis, Nile delta ; of *H. rolandi* Sauvage (1881) from Zibane,

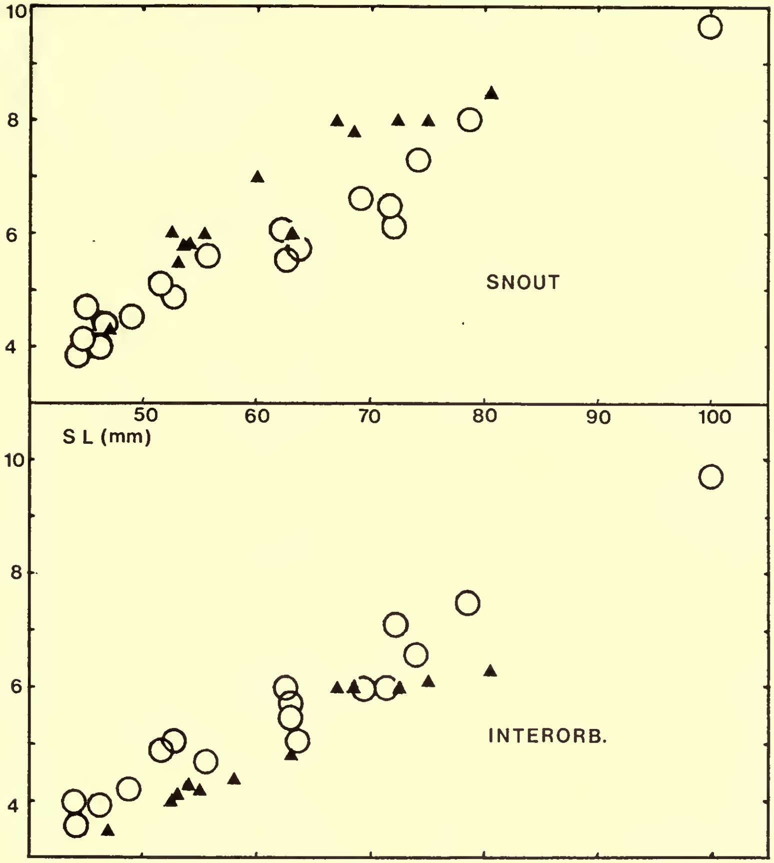


Fig. 3. Comparison between *H. fugax* (▲) and *H. bimaculatus* (○) in length of snout and interorbital width (in mm).

Constantine, Algeria ; *H. saharae* Sauvage (1880b) from near Touggourt ; and the large specimens that are the syntypes of *H. guttatus* Günther, of unknown locality. These names have been regarded as synonyms of *H. bimaculatus* (by Pellegrin, 1904 : 219, and Boulenger, 1915 : 431) and we are satisfied that *H. fugax* is distinct from them all.

ACKNOWLEDGEMENTS

We are grateful to Mr Paul L. Loiselle for communicating to us his views on the species of *Hemichromis* and particularly his opinion that the type of *H. bimaculatus*, which he has seen, is the species to which we have attributed the name. We also thank Dr G. Corbet and Dr P. H. Greenwood for reading the script and suggesting improvements.

MATERIAL EXAMINED

Hemichromis fugax	SL (mm)	Locality	Collector
BMNH 1976.1.28.1 (holotype)	72	Forest stream, Kassewe Forest Reserve, S.L.	A. I. Payne
BMNH 1976.1.28.6–7 (paratypes)	66, 76	Forest stream, Kassewe Forest Reserve, S.L.	A. I. Payne
BMNH 1976.1.28.2–3 (paratypes)	41, 70	Gbangbar system nr Moyamba, S.L.	A. I. Payne
BMNH 1971.8.13.24 (paratype)	43	Stream nr Njala, S.L.	A. I. Payne
BMNH 1976.1.28.4–5	45, 46·5	nr Moyamba, S.L.	A. I. Payne
BMNH 1976.1.28.8	72	River Taia, nr Njala, S.L.	A. I. Payne
BMNH 1976.1.28.9	53	Kassewe, S.L.	A. I. Payne
BMNH 1976.1.28.10–13	52–65	River Tabé, S.L.	A. I. Payne
BMNH 1915.5.27.21–23	40–80	'Victoria, S.L.'	N. W. Thomas
BMNH 1958.9.18.224–9	21–22·5	Potoru, S.L.	T. S. Jones
BMNH 1972.3.16.11–12	28, 59	50 km from Monrovia, Liberia	E. Roloff
Hemichromis bimaculatus			
BMNH 1888.10.19.23–32	24–74·5	Freetown, S.L.	R. Dinzey
BMNH 1899.11.25.4	100	Mountain stream, Freetown, S.L.	Hopkins
BMNH 1915.5.19.28–30	48·5–72	North Sherbro District, S.L.	N. W. Thomas
BMNH 1915.5.27.24	63	'Victoria, S.L.'	N. W. Thomas
BMNH 1950.9.22.50–70	22·5–71	Lake Kwarko, S.L. (7°18′N, 11°59′W)	T. S. Jones
BMNH 1958.9.18.219–222	45·5–89	Black 'River', Sherbro Is., S.L.	T. S. Jones
BMNH 1958.9.18.223	25·3	Bonthe, S.L.	T. S. Jones
BMNH 1958.9.18.230–239	22–36	Bonthe, S.L.	T. S. Jones
BMNH 1958.9.18.240–1	27, 33	RoKupr, S.L.	T. S. Jones
BMNH 1969.11.19.20–21 (3 fishes)	20·5, 62·5, 68	19 km from Monrovia, Liberia	C. Steiner
BMNH 1928.7.3.112–116	29·5–45·5	Kiyawa River, nr Katagum, Nigeria	Ll. Lloyd
BMNH 1930.3.22.276–284 (13 fishes)	15·5–44·5	Kiyawa River, nr Katagum, Nigeria	Ll. Lloyd
BMNH 1884.5.2.3–4 (syntypes of *H. saharae*)	39·5, 41·0	'Oued Rhir Constantine'	Mus. Hist. Nat. Paris
BMNH 1884.5.2.5–7 (syntypes of *H. rolandi*)	41·2–44·0	'Oued Rhir, Constantine, Algeria'	Mus. Hist. Nat. Paris
BMNH 1898.2.15.1 (syntypes of *H. letourneuxi*)	47·5, 51·0	Lake Mareotis, Egypt	Mus. Hist. Nat. Paris
BMNH 1860.4.19.3–4 (syntypes of *H. guttatus*)	90·7, 95·5	?	Stevens (purchased)

NOTE ON THE LOCALITIES

Most of the localities mentioned can be found on a modern map and by reference to our Fig. 4, but with two we had difficulty.

'Victoria, Sierra Leone.' The *Official Standard Names Gazetteer* gives the position of three such places, but in the maps consulted by us only those of an early *Handbook of Sierra Leone* (Goddard, 1925) mark any of them, and this only one, nearest to the Gazetteer reference 7°39′N, 12°20′W. This is a very small place a short way inland at the latitude of the north end of Sherbro Island, north of the delta of River Jong. Among the other fishes sent from this address was one '*Psettus sebae*', which confirms it as a locality near the coast.

Potoru. This also has three references in the Gazetteer, but the probable one is some 8 km west of River Moa at its expanded part. This is the only one marked

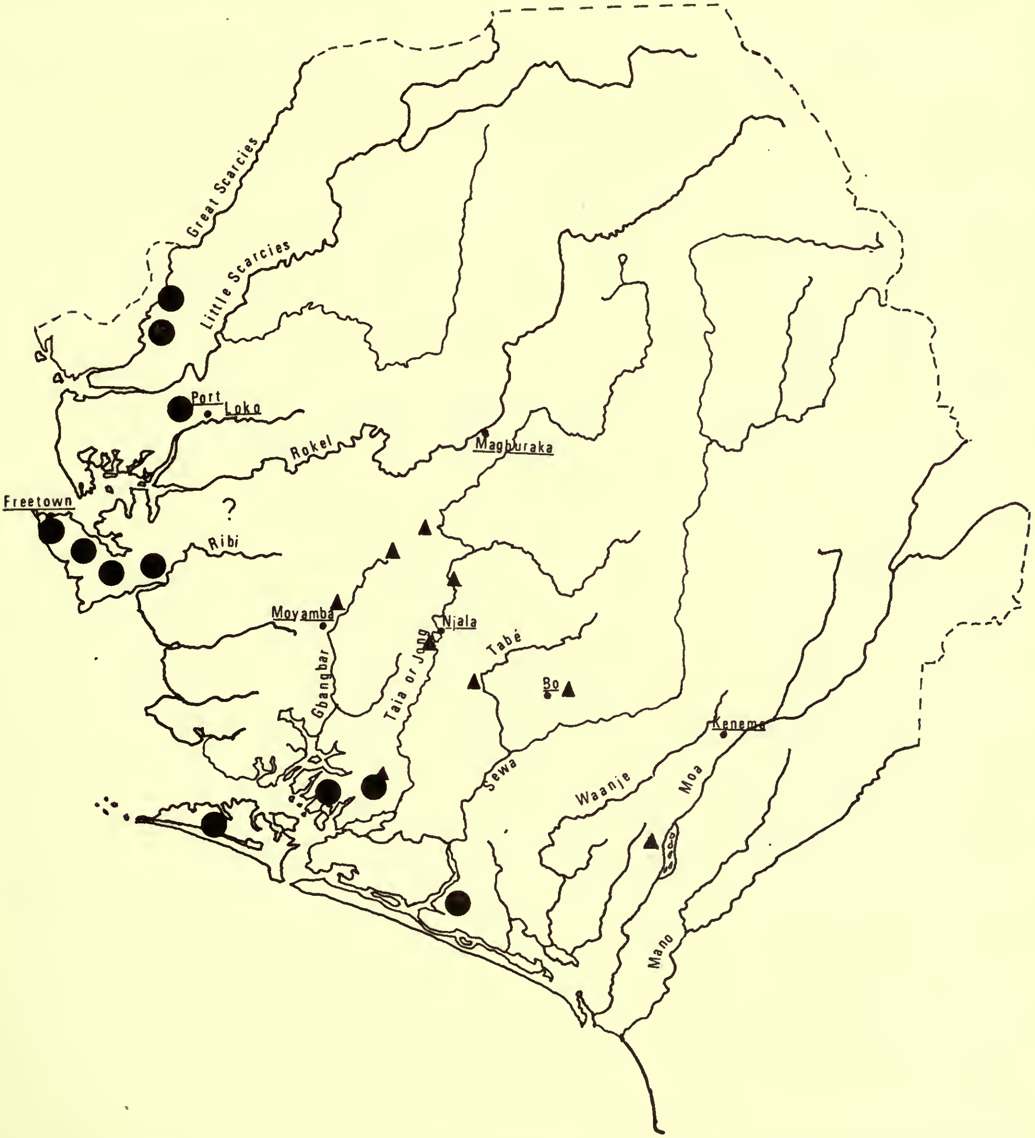

Great Scarcies
Little Scarcies
Port Loko
Rokel
Magburaka
Freetown
?
Ribi
Moyamba
Njala
Gbangbar
Taia or Jong
Tabé
Bo
Kenema
Sewa
Waanje
Moa
Mano

FIG. 4. The site records of *H. fugax* (▲) and *H. bimaculatus* (●) in Sierra Leone. At one site (?) fishes that were probably *H. bimaculatus* were observed but no specimens were taken.

on a map of 1950 (Director of Colonial Surveys, London), the period when Mr Jones was resident in Sierra Leone. It is also marked on the American 1 : 1 000 000 map NB 29 ser. 1301.

'Oued Rhir, Constantine.' This is the locality given in the register of BMNH for specimens of both *H. saharae* and *H. rolandi*. The original descriptions give for *H. saharae* 'Sahara, aux environs de Touggourth' and for *H. rolandi* 'Zibans, Sahara, Province de Constantine.' Both these localities are probably in the catchment area of Oued Rhir and Chott Melrhir. These and the specimens of *H. letourneuxi* in the BMNH are listed as 'types' by Boulenger (1915). Other syntypes remain in Paris.

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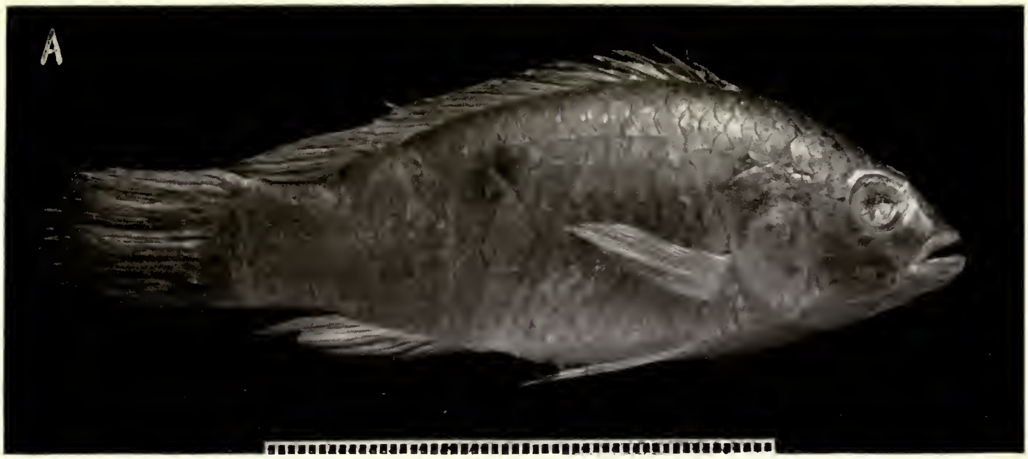
PLATE 1

(A) *Hemichromis bimaculatus* from Bonthe. (B) *H. fugax* holotype. (C) *H. fugax*, a Liberian specimen. All to the same scale. Photo BMNH.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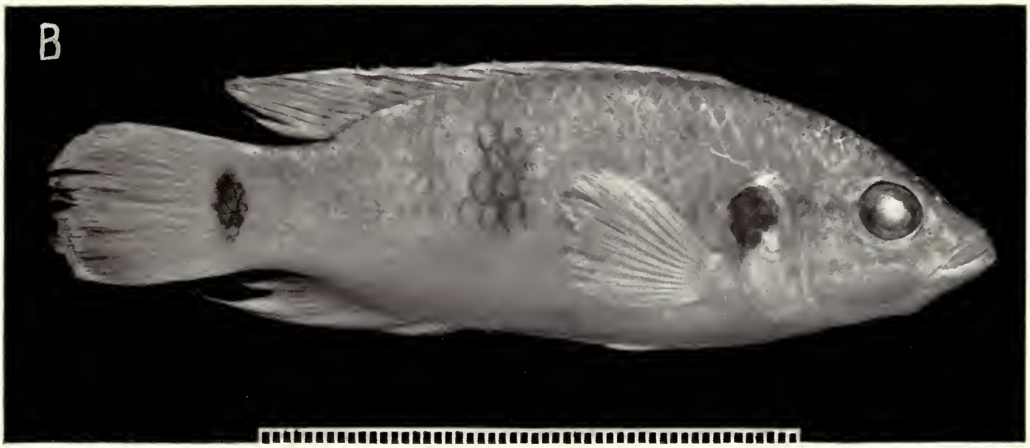
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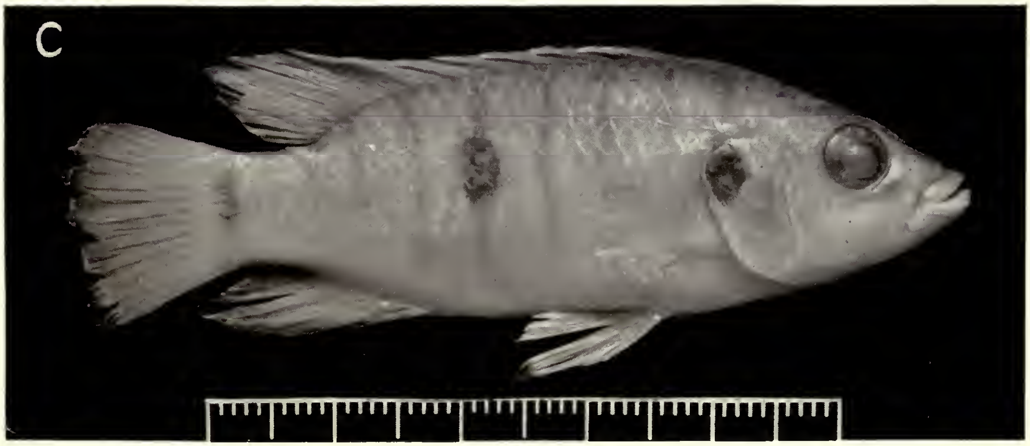
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A POSSIBLE INTERGENERIC CYPRINID HYBRID FROM LAKE TANGANYIKA

By K. E. BANISTER

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SYNOPSIS

A series of fishes from Lunkungwe (Lake Tanganyika) were found to have characters intermediate between two endemic species, *Barbus tropidolepis* and *Varicorhinus tanganicae*. The likelihood of a hybrid origin for the Lunkungwe fishes is discussed and comments are made on the validity of the generic separation of the two putative parent species.

INTRODUCTION

During 1968 and 1969, Dr E. K. Balon of the Zoology Department, University of Guelph, Canada, collected eleven specimens of a cyprinid fish from Lunkungwe (5°45'S, 29°55'E), Lake Tanganyika. The largest specimen (133 mm SL) is now in the Museum of Zoology, University of Michigan (MZM 191573). The other ten specimens are in the Royal Ontario Museum (ROM 28132 and 28167).

These fishes are not referable to any known cyprinid species from Lake Tanganyika but are morphologically intermediate between *Varicorhinus tanganicae* and *Barbus tropidolepis*, species endemic to the Lake Tanganyika basin. From the data presented below it will be seen that the eleven Balon fishes are unlikely to represent extreme examples of either *Varicorhinus tanganicae* or *Barbus tropidolepis*.

In this paper I intend to put forward the hypothesis that these eleven fishes are hybrids between *Barbus tropidolepis* and *Varicorhinus tanganicae*.

Much of the evidence and discussion is, of necessity, similar to that given in Banister (1972). In that case the discovery of some fishes morphologically intermediate between *Barbus somereni* and *Varicorhinus ruwenzorii* was used as evidence for the hypothesized hybridization of these two species. Without breeding experiments, hybridization cannot be proved, but the circumstantial evidence is worth examining. Previously (Banister, 1972) I noted that the boundary between the African representatives of the genus *Barbus* and the genus *Varicorhinus* is

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vague. It has been shown (Groenewald, 1958; Gaigher, 1975) that under certain conditions some species of *Barbus* can change their mouth form and simulate the mouth type present in *Varicorhinus* species. Without an examination of more trenchant characters and without a knowledge of the previous history of the specimen, an individual fish could be placed with equal justification in either genus as the two genera are currently accepted (e.g. the definitions of Boulenger, 1909, and Jubb, 1968). These two definitions are, in the light of the known variation of some species, inadequate. The morphological intermediates described here, and *Barbus alluaudi* (Banister, 1972), raise further doubts about whether some species have been correctly assigned to the genus *Varicorhinus*. Work is in progress on the limits of the genera *Barbus* and *Varicorhinus*.

NOTES ON COUNTS AND MEASUREMENTS

The standard length (SL) was taken in the usual manner. The lateral line count (LL) was taken from the first pore-bearing scale behind the head to the scale lying lateral to the end of the hypurals. The body depth (D) is the maximum body depth, usually to be found just in front of the dorsal fin. The anterior limit for the head length (H) and snout length (Snt) was the premaxillary symphysis, with the premaxillae retracted. The posterior limit for the snout is the anterior margin of the orbit and for the head length is the most posterior part of the bony edge of the operculum. The term mouth width (MW) refers to the width across the lower jaw at the level of the angle of the mouth. The pectoral fin length (Pct) is the total length of the fin, measured in a straight line from the base of the first fin ray to the distal extremity of the fin. The measurements were taken in this way because of the ease of so doing with dial calipers, which were used on all fish except the smallest when dividers were used. The caudal peduncle length (CPl) is the horizontal distance from the posterior angle at the base of the last anal fin ray to the end of the hypurals and the caudal peduncle depth is the least depth of that part. The interorbital width (IO) was measured as the least distance between the bony edges of the interorbital space. The eye diameter (I) is the horizontal diameter of the visible part of the eye. Dsp symbolizes the height of the dorsal fin from the base of the first spine to the distal extremity of the longest fin ray. With any measurements which were repeatable on both sides of the fish (e.g. the anterior barbel, Ab or posterior barbel, Pb) the larger was taken except in cases where a deformity was obvious.

The majority of measurements were taken to the nearest millimetre, the exceptions were some measurements on small fishes; these were taken to the nearest half millimetre. The mean is symbolized by $\bar{x}$, the standard deviation by s.d., the standard error by s.e. and the number of fish in the sample by n.

THE PUTATIVE HYBRIDS

DESCRIPTION. The description is based upon 11 fishes of 133, 105, 77, 69, 66, 59, 59, 58, 55, 55, 55 mm SL from Lunkungwe, Lake Tanganyika, ROM 28132, 28167 and MZM 191573. The largest specimen is shown in Fig. 1.

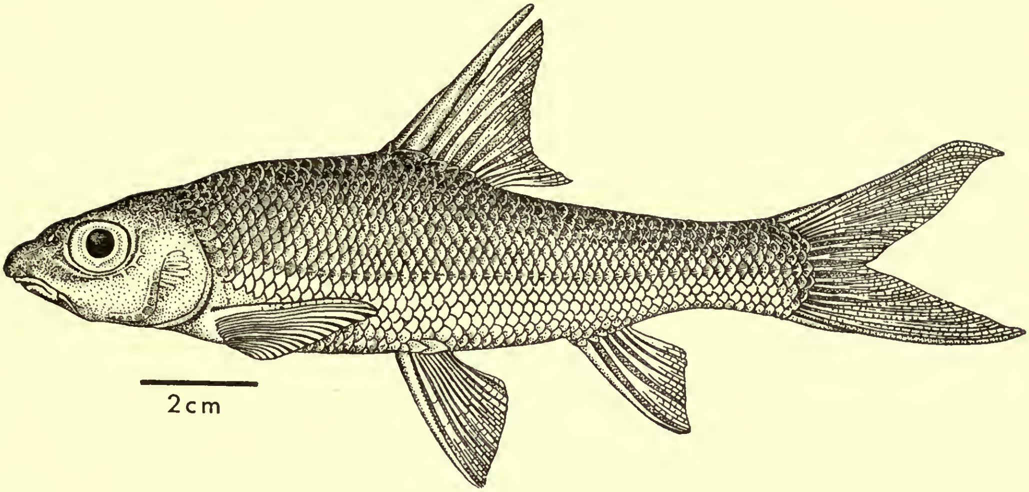

FIG. 1. The largest putative hybrid, a fish of 133 mm SL.

	x	s.d.	s.e.	range
SL	–	–	–	55 –133 mm
D	25·8	1·5	0·4	23·5–28·6
H	27·0	1·7	0·5	23·5–29·3
I	8·5	0·5	0·2	7·8– 9·3
IO	7·5	0·6	0·2	6·8– 8·8
MW	6·9	0·6	0·2	6·4– 8·5
Pct	21·3	1·1	0·3	19·6–28·6
CPl	18·9	1·5	0·5	15·3–21·0
CPd	10·9	0·7	0·2	9·8–11·7
Snt	7·8	1·1	0·6	6·8– 9·8
Ab	1·8	0·3	0·1	1·5– 2·3
Pb	3·2	0·5	0·2	2·5– 3·8

Unless stated otherwise, all measurements are expressed as a percentage of the standard length.

The body is compressed, with smooth dorsal and ventral profiles. The deepest part of the body is just in front of the dorsal fin. The eye is large, protuberant and just visible in ventral view. The fleshy, rounded snout terminates in a rostral flap which is level with, but does not overhang, the mouth.

The anterior margin of the lower jaw is gently curved ; it has a sharp edge but lacks the conspicuous horny sheath present in specimens of *Varicorhinus tanganicae* (Pl. 2). Nevertheless, it has a shiny, padded appearance suggesting that a tough integument is present. The lower jaw is only slightly wider at its articulation than it is distally. The ventral face of the lower jaw is concave and the skin in this and the contiguous gular region bears numerous small papillae.

No lateral line pores are visible on the ventral surface of the lower jaw. There are two pairs of barbels. The short anterior barbels are usually hidden in a groove between the ventral edge of the lachrymal bone and lips. In the second largest specimen (105 mm SL) a few isolated tubercles are present on the skin of the snout and the dorsal half of the lachrymal bone. The tubercles are about four times the diameter of the lateral line pores of the lachrymal bone.

In nine of the specimens the gill filaments could be seen clearly through a transparent zone in the centre of the opercular bone. In the other two fishes a dark patch of pigment was present through which the gill filaments could only just be discerned.

The peritoneum is dark grey/brown in the two specimens examined. The alimentary canal is narrow and much convoluted. There are 20+21 (f1), 20+22 (f3), 21+20 (f1), 21+21 (f2), 21+22 (f3) or 22+21 (f1) vertebrae including those comprising the Weberian mechanism.

From radiographs it can be seen that the angle of insertion of the pectoral fin is different in the three samples of fishes. The angle of insertion of the pectoral fin is here defined as the angle that a line through the mid-point of the first and last pectoral radials subtends with a line from the mid-point of the occipital condyle to the mid-point of the ural centrum. In the largest fish this angle is 30° ; in the other specimens it varied from 21° to 41°.

Dorsal fin. The dorsal fin has 4 simple rays and 9 (f11) branched rays. The last simple ray is thickened into a straight smooth spine ($\bar{x}=26{\cdot}3$, s.d.$=1{\cdot}5$, s.e.$=0{\cdot}5$, range$=23{\cdot}8-28{\cdot}5$). A low sheath of scales is present at the base of the dorsal fin.

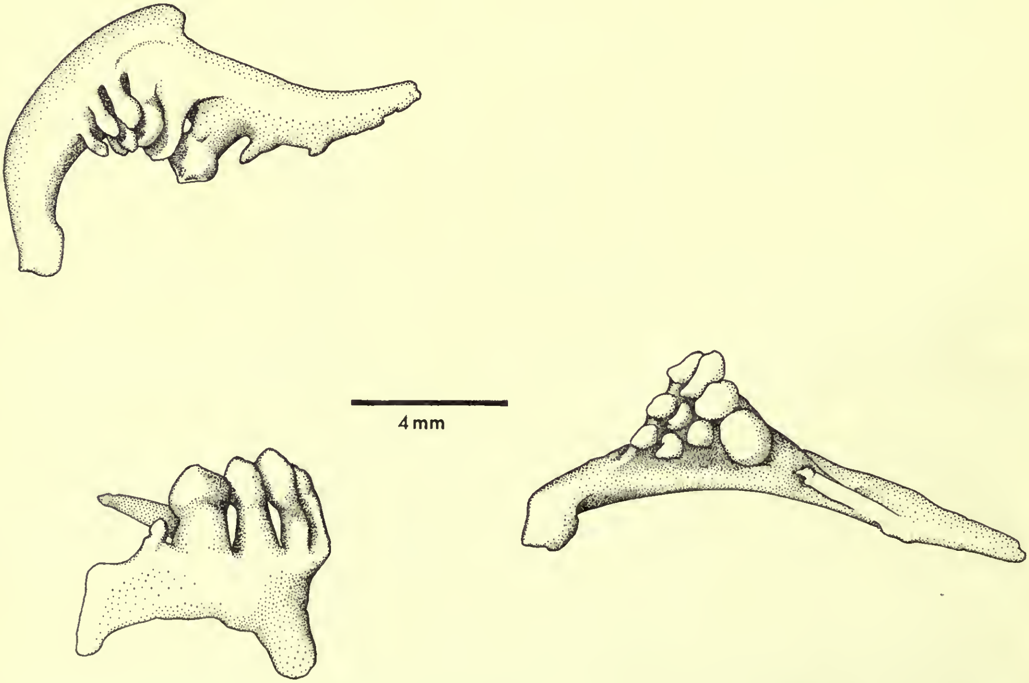

FIG. 2. The right pharyngeal bone of the largest hybrid.

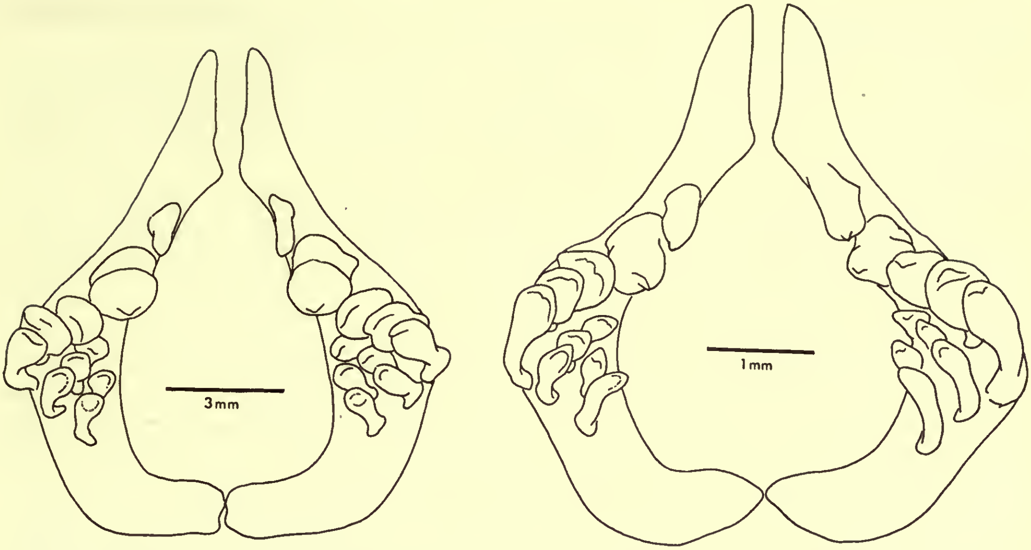

FIG. 3. Occlusal views of the pharyngeal bones of hybrids of 133 and 59 mm SL to show the arrangement of the tooth rows.

This sheath is highest anteriorly and is reduced to the level of the body contour by about the seventh or eighth branched ray. The origin of the dorsal fin is in advance of the pelvic fin.

Squamation. In the lateral line series there are 46 (f1), 47 (f1), 49 (f2), 50 (f1), 51 (f1), 52 (f2), 53 (f1), 54 (f1) or 56 (f1) scales. From the dorsal mid-line to the lateral line there are 10½ (f5) or 11½ (f6) scales. From the lateral line to the ventral mid-line there are 10½ (f2), 11½ (f3) or 12½ (f3) scales. This count was unobtainable on some specimens. Between the lateral line and the base of the pelvic fin there are 5½ (f5), 7 (f1) or 7½ (f4). Around the mid-point of the caudal peduncle there are 22 (f5) or 24 (f4) scales. The scales bear slightly diverging striations (Fig. 5).

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2. The right pharyngeal bone of the largest specimen is shown in Fig. 2. The first (anterior) tooth of the inner row is short and slender and its alignment is more or less parallel with the adjacent edge of the second tooth. This tooth is large and stout with a mamilliform crown surmounted by a small recurved hook. The third, fourth and fifth teeth become progressively more slender and spatulate. The teeth of the second and third rows are smaller versions of the third, fourth and fifth teeth of the inner row. From the occlusal view of the pharyngeal bones the alignment of the middle and outer tooth rows can be seen. In about half of the specimens these two rows diverge from the first tooth of the middle row. In the rest of the specimens the rows are parallel. In two specimens one pattern is present on one bone and the others on its partner.

The mean tip-to-tip length of the pharyngeal bones of a specimen 105 mm SL is 10 mm and the mean length in a specimen of 59 mm SL is 6·3 mm. These figures should be compared with the measurements of the pharyngeal bones of equal-sized *Barbus tropidolepis* and *Varicorhinus tanganicae* (pp. 179 and 183).

Gill-rakers. There are 15 (f5), 16 (f5) or 18 (f1) gill-rakers on the lower limb of the first gill-arch. The shape of the gill-rakers is intermediate between those of the putative parents; i.e. they are moderately thick with a clubbed or T-shaped extremity.

Coloration. These colour notes are based on alcohol-preserved specimens. The smaller fishes are lighter than the larger fishes. The body colour is yellow-brown, darker on the back than below the lateral line. The belly in some specimens has a pink tinge. There is a dark, broad mid-lateral stripe 3 or 4 scales deep caused by a concentration of pigment along the posterior edge of alternate scales in the rows at the edge of the band and on all the scales of the central rows. A distinct mid-dorsal stripe is present in several specimens. These stripes become less distinct in larger fishes as the body colour becomes progressively darker. All but two of the specimens have a clear spot on the operculum. The dorsal fin has a dark margin in small fishes but this becomes progressively fainter in larger fishes.

DISTRIBUTION. All the specimens came from Lunkungwe, Lake Tanganyika. Dr Balon kindly provided the following details of the locality. The Lunkungwe River empties into a large bay on the eastern shore of central Lake Tanganyika about 100 km south of Kigoma in Tanzania. The river flows from the Kingwe mountains in a valley flanked by very steep foothills. The river gradient is steep. The width varies from 4 to 10 m, and there are rapids between rock outcrops and large boulders on the river bed. The fish were sampled about 2 km before the river empties into the lake. The river at this point flows swiftly but there are some pools with a plant resembling *Fontinalis* sp. The river is muddy when it empties into the lake and is bordered with reed thickets. The fish were poisoned with toxophene.

THE PUTATIVE PARENT SPECIES

Varicorhinus tanganicae (Boulenger, 1900)

Capoeta tanganicae Boulenger 1900 : 478.
Varicorhinus tanganicae : Boulenger, 1905 : 43 ; Poll, 1953 : 97.

LECTOTYPE. A fish of 282 mm SL from the north end of Lake Tanganyika, one of the two syntypes, BMNH reg. no. 1906.9.6:9–10. The lectotype is the largest of the two specimens, the smaller specimen being designated a paralectotype.

MATERIAL EXAMINED. Apart from the syntypes the following specimens were used in this study: BMNH1936.6.15:731–751 ; 1955.12.20:900–903 ; 1955.12.20:881.

DESCRIPTION. Two separate samples of *Varicorhinus tanganicae* from Lake Tanganyika have been measured. One sample, of 24 fish from 48 to 282 mm SL, is intended to show the morphometric and meristic variation of the species. The other sample consists of five fishes of 59, 59, 80, 104 and 139 mm SL which are all the specimens available close to the size range of the hybrids. These are included to enable a detailed comparison to be made limiting, as far as possible, any distortion from allometry.

Sample 1 (n = 24)

	x̄	s.d.	s.e.	range
SL	–	–	–	48 –282 mm
D	25·9	2·1	0·4	23·0–30·0
H	22·7	2·4	0·5	14·6–26·0
I	6·3	0·9	0·2	4·6– 8·3
IO	9·1	0·9	9·2	7·4–10·6
MW	8·0	0·5	0·1	7·1– 9·5
Pct	19·7	1·2	0·2	16·6–21·4
CPl	17·2	0·9	0·2	15·1–18·9
CPd	12·8	0·9	0·3	10·4–14·7
Snt	7·3	0·6	0·1	6·4– 8·3
Ab	+	–	–	–
Pb	+	–	–	–
Dsp	19·8	3·0	0·6	12·6–24·8

It should be noted that although two pairs of barbels are invariably present in the specimens examined they are minute in the large fishes. Consequently barbel lengths are not included in this sample but are included in the 59–139 mm SL sample below.

Sample 2 (n = 5)

	x̄	s.d.	s.e.	range
SL	–	–	–	59 –139 mm
D	26·3	1·2	0·5	25·0–28·0
H	24·8	2·0	0·9	22·3–27·1
I	7·3	0·3	0·1	6·9– 7·6
IO	8·8	0·3	0·1	8·5– 9·3
MW	8·7	0·5	0·2	7·9– 9·3
Pct	20·5	1·2	0·5	18·9–22·0
CPl	15·4	1·4	0·6	13·5–17·3
CPd	10·5	0·5	0·2	10·0–11·0
Snt	6·8	0·5	0·2	6·3– 7·5
Ab (n = 4)	1·3	1·0	0·5	0·1– 2·6
Pb	3·1	1·3	0·6	1·4– 5·1
Dsp	23·9	2·3	1·0	21·2–27·3

Unless stated otherwise all measurements are expressed as a percentage of the standard length.

The body is compressed and streamlined, with smooth dorsal and ventral profiles. The snout is fleshy and bluntly rounded. The rostral flap almost overlaps the margin of the upper jaw on the ventral surface of the snout. The eye is large and protuberant usually visible from below, a feature that is more conspicuous in smaller specimens. In fishes of less than about 60 mm SL the anterior edge of the lower jaw is gently curved and lacks a horny covering. The lower jaw is straight-edged in larger fishes and has a sharp horny cutting edge.

A series of six or seven lateral line pores is usually conspicuous on the skin of the ventral surface of each ramus of the lower jaw. Two pairs of small barbels are

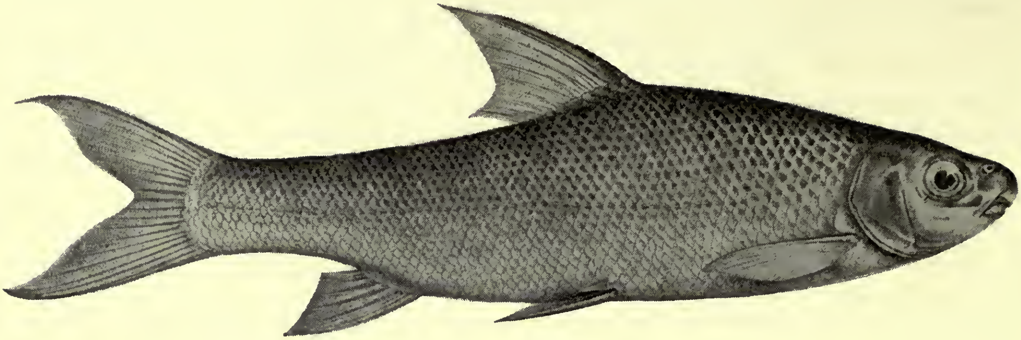

FIG. 4. *Varichorhinus tanganicae* (from Boulenger, 1901).

present. The anterior barbels can best be described as small prolongations of the postero-ventral corners of the rostral flap. The groove below the lachrymal bone is much narrower than in the Balon specimens. A few of the larger (more than about 200 mm SL) specimens have a scattering of small, poorly defined tubercles on the skin covering the lachrymal bone. The tubercles are non-contiguous and are about the same absolute size as those in the putative hybrids.

The peritoneum is dark grey-brown and the intestine is more convoluted than in the putative hybrids.

There are 20 + 21 (f1), 21 + 21 (f2), 21 + 22 (f4), 22 + 21 (f2) or 22 + 22 (f1) vertebrae in the ten specimens radiographed.

The angle of insertion of the pectoral fin varies between 37° and 51° in the ten specimens examined.

Dorsal fin. There are 4 unbranched rays and 8 (f4), 9 (f17) or 10 (f3) branched rays. The fourth simple ray is ossified into a straight smooth spine. The shape of

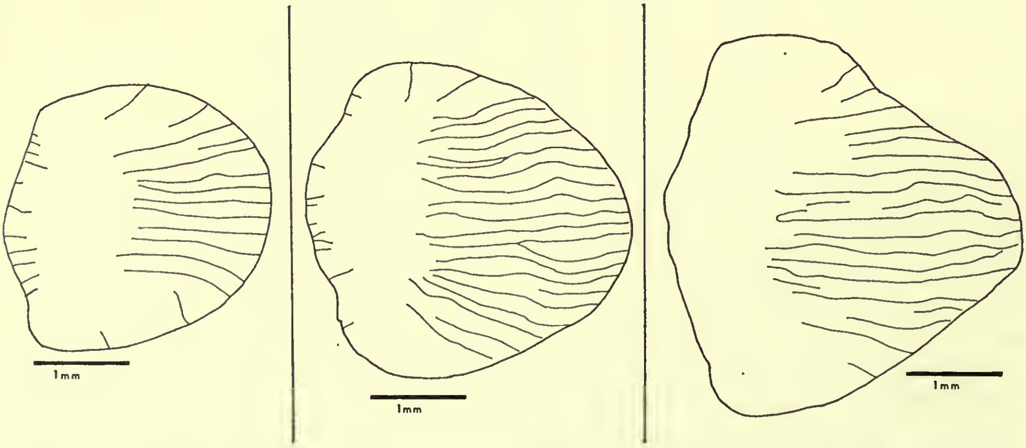

FIG. 5. A scale of a specimen of *Varichorhinus tanganicae* of 139 mm SL (left) a hybrid of 133 mm SL (centre) and a *Barbus tropidolepis* of 134 mm SL (right).

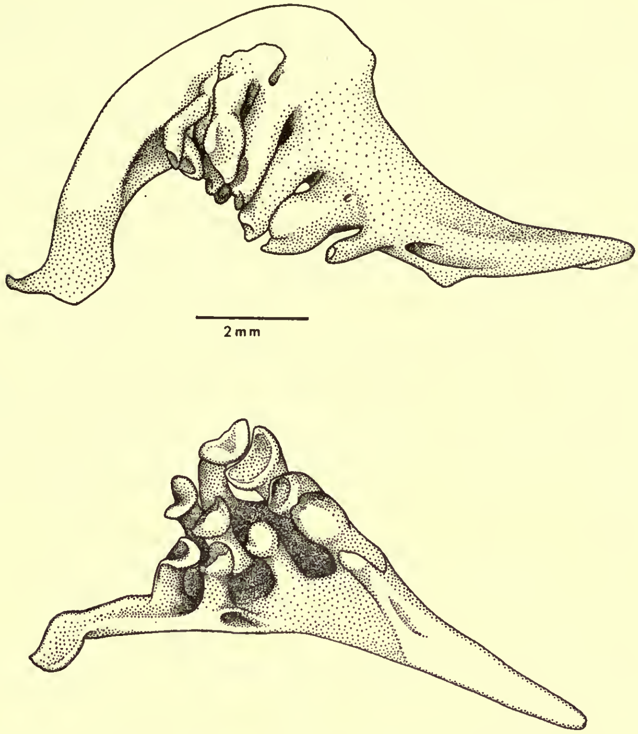

FIG. 6. The right pharyngeal bone of *Varicorhinus tanganicae* of 139 mm SL.

the dorsal fin is shown in Fig. 4. The anterior half of the base of the dorsal fin is surrounded by a low sheath of scales. The origin of the dorsal fin is in front of the origin of the pelvic fin.

Squamation. There are from 57 to 67 scales in the lateral line series: 57 (f2), 58 (f1), 60 (f2), 61 (f4), 62 (f2), 63 (f4), 64 (f4), 65 (f4), 67 (f1). There are 12½ (f12), 13 (f9) or 14½ (f3) scale rows from the dorsal mid-line to the lateral line. Between the lateral line and the ventral mid-line there are 12½ (f1), 13½ (f5), 14½ (f6), 15½ (f5), 16½ (f2) or 17½ (f1) scale rows. These scales could not be counted on some specimens. From the lateral line to the base of the pelvic fin there are 8 (f10), 9 (f12), 10 (f1) or 11 (f1) scales. Around the least circumference of the caudal peduncle there are 29 (f1), 30 (f5), 31 (f3), 32 (f6) or 33 (f2) scales.

The striations on the scales are radiate, but they tend to be more divergent in smaller fishes than in larger ones.

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2 (Fig. 6). The teeth are slender and the posterior teeth in each row have spatulate crowns. The teeth are arranged in three parallel rows. The mean tip-to-tip measurement of the pharyngeal bones of a specimen of 104 mm SL is 8·9 mm and of a 60 mm SL specimen 6·0 mm.

Gill-rakers. In the 14 specimens examined the number of gill rakers on the lower limb of the first gill arch is 17 (f1), 18 (f4), 19 (f7) or 20 (f2). The gill rakers are slender, conical and bear small lateral projections.

Coloration. Live fishes were described by Poll (1953) as brown to grey on the back, paler ventrally. A silver sheen is usually present and the fins are pale grey. Preserved specimens are usually a pale yellow/brown in colour although the larger specimens tend to be greyer.

DISTRIBUTION. This species is confined to the Lake Tanganyika basin. According to Poll (1953) it is found in both the lake and the affluent rivers, even in the rapids of the inflowing streams. In the lake it is commonest in rocky areas near to the mouths of streams. It ascends rivers to breed. Small fishes (less than 80 mm SL) are rare in the lake and seem to spend the early part of their lives in the streams. In both the lake and the feeder streams *Varicorhinus tanganicae* is found feeding in sandy, gravelly or rocky regions, rummaging for insect larvae. Ostracods, worms and diatoms mixed with grains of sand are also found in the alimentary canal (Balon, pers. comm.).

Barbus tropidolepis Boulenger, 1900

For synonymy see Banister (1973).

MATERIAL EXAMINED. In addition to the syntypes, the following specimens were examined: BMNH1955.12.20:737–740; 1955.12.20:775–792; 1955.12.20:795–799; 1955.12.20:806–815; 1955.12.20:1169–1171.

DESCRIPTION. Two separate samples of *Barbus tropidolepis* were measured. The first, a sample of 47 fishes from Lake Tanganyika, are between 99 and 365 mm SL and serve to show the variation of morphometric characters in the species (taken from Banister, 1973). The second sample is of ten fishes and represents all the available specimens within the size range of the putative hybrids. These ten fishes are of 56 (2), 59 (2), 60, 66, 69, 75, 105 and 134 mm SL.

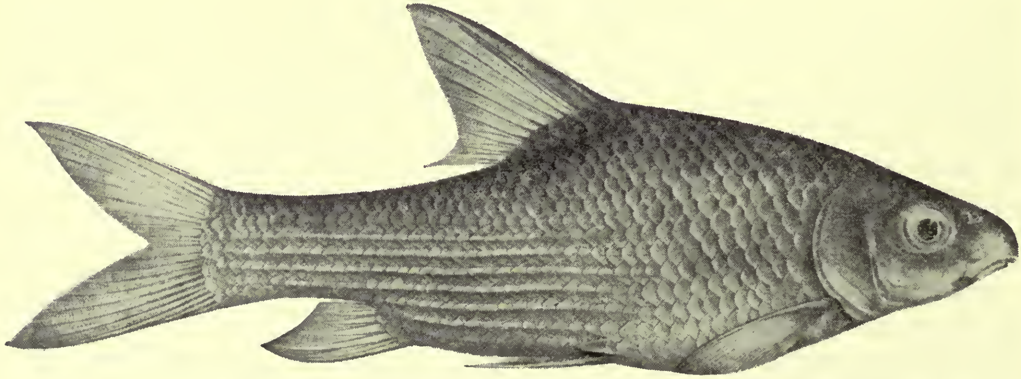

FIG. 7. *Barbus tropidolepis* (from Boulenger, 1901).

Sample 1 (n = 47)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	99 –365 mm
D	28·8	2·7	0·6	25·0–33·7
H	27·0	1·4	0·3	24·8–30·1
I	9·4	1·3	0·3	7·0–11·0
IO	9·0	1·5	9·3	7·4–11·4
MW	6·4	0·8	0·2	5·2– 8·8
Pct	20·8	1·0	0·2	19·1–23·9
CPl	14·9	1·2	0·3	12·9–17·7
CPd	11·7	0·9	0·2	10·1–13·7
Snt	8·4	1·0	0·2	5·2– 9·3
Dsp	25·8	2·7	0·6	20·8–30·0

Sample 2 (n = 10)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	56 –134 mm
D	26·3	2·2	0·7	23·4–30·6
H	27·2	0·7	0·2	25·9–28·8
I	8·8	0·6	0·2	8·2–10·2
IO	8·7	0·6	0·2	7·6– 9·7
MW	5·9	0·5	0·1	5·1– 6·7
Pct	20·4	1·7	0·5	16·6–22·6
CPl	14·3	1·0	0·3	12·0–15·3
CPd	11·2	0·6	0·2	10·5–12·1
Snt	7·3	0·6	0·2	6·5– 8·2
Dsp	28·2	1·5	0·5	25·0–30·6

All measurements are expressed as a percentage of the standard length unless stated otherwise.

The body has a compressed, fusiform shape. The blunt snout lacks a rostral flap. Only a very shallow groove is present between the edge of the lachrymal bone and the snout. The eye is protuberant and conspicuous in ventral view.

The mouth is subterminal. The lower jaw is narrow with a soft, curved, anterior margin. The lower lip is often discontinuous medially. A few specimens have the lips slightly thickened. The gular surface is deeply folded. There is no anterior barbel and the posterior barbel is represented by a very small papilla. Although invariably present, this barbel is too short to measure accurately.

Small, scattered tubercles are present on the skin covering the dorsal part of the lachrymal bone as well as between the orbit and the nostrils. The tubercles are smaller than those of *Varicorhinus tanganicae* or the Balon specimens. In common with *Varicorhinus tanganicae* a series of 6 or 7 lateral line pores is conspicuous on the ventral surface of each ramus of the lower jaw. The peritoneum is mid-brown in colour.

In the 14 specimens radiographed there are 18 + 22 (f1), 19 + 21 (f4), 19 + 22 (f8) or 19 + 23 (f1) vertebrae. The angle of insertion of the pectoral fin varies from 12° to 23° in the specimens radiographed.

Dorsal fin. There are 4 unbranched rays (not 3 as reported by Boulenger, 1911, and Worthington & Ricardo, 1937). The last unbranched ray forms a smooth straight spine. There are 9 (rarely 10) branched rays. The dorsal margin of the dorsal fin has a characteristic shape which can be seen in Fig. 7. The origin of the dorsal fin is directly above or slightly in advance of the pelvic fins.

Squamation. There are from 39 to 44 scales in the lateral line series: 39 (f2), 40 (f9), 41 (f11), 42 (f13), 43 (f9), 44 (f3). There are $8\frac{1}{2}$ (rarely $7\frac{1}{2}$) scale rows between the dorsal mid-line and the lateral line and $8\frac{1}{2}$ (rarely $7\frac{1}{2}$, very rarely $9\frac{1}{2}$) scale rows between the lateral line and the ventral mid-line. Around the least circumference of the caudal peduncle there are 16 (f34), 17 (f6) or 18 (f7) scales. The ridges of fat that may occur on the scales of this species (see Banister, 1973) do not occur in the putative hybrids nor in *Varicorhinus tanganicae.* The scale striations are more or less parallel. The posterior margin of each scale is markedly lobate.

Pharyngeal bones and teeth. The pharyngeal teeth usually number 2.3.5–5.3.2. The first tooth of the inner row is very small and may be absent. When absent, its locus is marked by a small pinnacle of bone. The second tooth of the inner row is stout with a molariform crown. The remaining three teeth in this row become progressively thinner. The crowns of especially the third and fourth teeth are almost as wide as that of the second tooth but are not so long, i.e. they are kidney-shaped when viewed from an occlusal position (see Fig. 9).

The alignment of the second and third rows is characteristic in that the first tooth of the second row is displaced slightly so that the second and third tooth rows

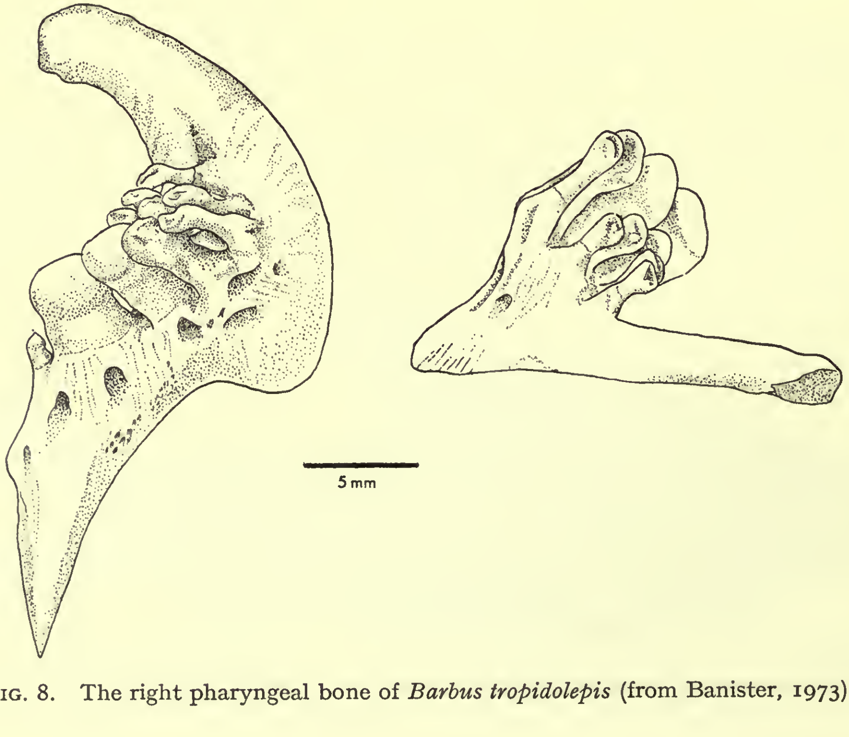

Fig. 8. The right pharyngeal bone of *Barbus tropidolepis* (from Banister, 1973).

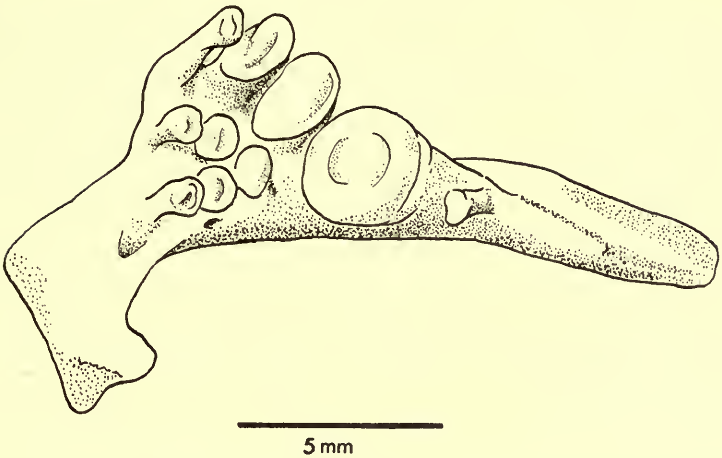

FIG. 9. Occlusal view of the right pharyngeal bone of *Barbus tropidolepis* (from Banister, 1973).

appear to radiate from it, rather than lying parallel to each other. The mean tip-to-tip length of the pharyngeal bones from a specimen of 105 mm SL is 13·5 mm and the mean for the pharyngeal bones from a fish of 60 mm SL is 7·5 mm.

Gill-rakers. There are 13 (f10), 14 (f4) or 15 (f2) gill-rakers on the lower limb of the first gill-arch in the 16 specimens examined. The gill-rakers are broad based with the outside edge produced forwards as a hook.

Coloration. The colour of live fishes, as described by Poll (1953), is grey or olive on the back, lighter ventrally. There is no noticeable colour pattern. Preserved fishes are brown on the body. Small specimens (less than about 90 mm) have a dark margin to the dorsal fin ; otherwise the fins are pale brown.

Habitat. This species is found in Lake Tanganyika to a depth of 25 m. It also occurs in feeder streams, especially in the breeding season (Poll, 1953).

DISCUSSION

There are three possible ways of regarding Balon's anomalous fishes. They could represent a new species, they could be hybrids or they could represent extreme representatives of a known species. The Balon specimens are very much rarer in the wild than either *Barbus tropidolepis* or *Varicorhinus tanganicae* and they have only been found at one locality. Hubbs, Hubbs & Johnson (1943) quote, for two species of North American Catostomidae captured in the same river system, a proportion of hybrids to parents of 4·2 and 6·4%. They also state that some hybrids are much rarer and the proportion may be about 1%.

There is no quantitative information available about the Balon specimens. However, Balon (pers. comm.) has stated that they occur with *Barbus tropidolepis* and *Varicorhinus tanganicae* and are very much rarer than either. This information, coupled with the conspicuous morphological intermediacy between *Barbus tropidolepis* and *Varicorhinus tanganicae* possessed by the Balon fish, suggests it is unlikely that they represent a true species.

The consistent differences between *Barbus tropidolepis* and *Varicorhinus tanganicae* in morphometric and meristic characters leave no doubt as to their specific distinctness. The differences in mouth form and associated feeding structures could arguably be the result of particular responses to the environment (Groenewald, 1958), but this is unlikely because of the discrete differences in other, and apparently unrelated, characters.

The morphometric intermediacy of aquarium-bred, and thus indisputable, hybrids has often been noted (e.g. Holčik & de Witt, 1962a, b; Hubbs & Miller, 1952). Hubbs (1955) described the morphological intermediacy of hybrids in the wild. Berry & Low (1970) and Hubbs (1955) advocate intermediacy as a very significant character of hybridization.

Unfortunately, the supporting evidence for hybridization that was used in the case of *Barbus alluaudi* (Banister, 1972) has not been available in this instance. For example, I have not been able to examine the gonads because of their inadequate preservation and I have but little information of the frequency of the occurrence of the Balon fishes in the wild. Therefore, the case rests solely on morphological evidence.

The 11 Balon fishes have 45–56 scales in the lateral line series. This is a wide range for a small sample. There are only five species of large *Barbus* and *Varicorhinus* in Lake Tanganyika. *Barbus tropidolepis* has 39–44 (n=47) scales; *Varicorhinus tanganicae* has 57–67 (n=24); *Varicorhinus leleupanus* has 42 or 43 (n=2); *Barbus platyrhinus* has 38–41 (n=7); and *Barbus caudovittatus* has 24–30 (n=47). Considering just the lateral line scale counts, no overlap exists between any of the recognized species and the Balon specimens; which alone tends to render unlikely the hypothesis that these specimens represent extreme forms of any known species.

Only one of the five species of *Varicorhinus* and large *Barbus* in Lake Tanganyika has smaller scales than the fishes under consideration, i.e. *Varicorhinus tanganicae* with 57–67 scales in the lateral line series. This species, therefore, is a certain candidate as one of the parents of the putative hybrids.

On the basis of the scales alone, *Barbus caudovittatus* can surely be eliminated as the other parent, but this still leaves *Barbus platyrhinus*, *Barbus tropidolepis* and *Varicorhinus leleupanus*. The bulky body of *Barbus platyrhinus* is not reflected in the streamline shape of the Balon fishes. A hybrid between *Varicorhinus leleupanus* and *Varicorhinus tanganicae* would be very likely to have a wide, horny-edged 'sector' mouth. The Balon fishes do not have a wide, horny-edged 'sector' mouth. Furthermore, *Varicorhinus leleupanus* has not been recorded from the Lunkungwe area of Lake Tanganyika. In the wild, the Balon fishes occur together with both *Barbus tropidolepis* and *Varicorhinus tanganicae*.

The range, mean and one standard deviation each side of the mean for seven morphometric characters of the putative hybrids and probable parent species are given in Table 2. The characters chosen (H, I, IO, MW, Dsp, Ab, Pb) are the same as were considered when discussing the hybrid origin of *Barbus alluaudi*

(Banister, 1972). The choice was made partly for comparison with the *Barbus alluaudi* situation and partly because these are the only morphometric characters in which the putative parent species differ significantly from each other and/or from the hybrid. The samples of *Barbus tropidolepis* and *Varicorhinus tanganicae* are from the same size range as the putative hybrids.

The number of vertebrae and the number of gill-rakers on the lower limb of the first gill-arch in the Balon fishes are intermediate between those of the putative parents (Table 1). The pharyngeal bone length and the angle of insertion of the pectoral fin show the same intermediacy, as does the alignment of the pharyngeal teeth.

TABLE 1

	Total no. of vertebrae	Gill-rakers	Pectoral insertion angle
B.t.	40–42 (n = 14)	13–15 (n = 16)	12–23° (n = 9)
Hyb.	40–43 (n = 11)	15–18 (n = 11)	21–40° (n = 11)
V.t.	41–44 (n = 10)	17–20 (n = 14)	37–51° (n = 12)

Mean length of pharyngeal bones

	SL (mm)	Ph. length (mm)
V.t.	60	6·0
V.t.	104	8·9
Hyb.	59	6·3
Hyb.	105	10·0
B.t.	60	7·5
B.t.	105	13·5

The possibility that the Balon fishes represent an extreme example of either putative parent species must now be considered. The techniques of Schultz & Schaeffer (1936) and of Hubbs, Hubbs & Johnson (1943) have been used to evaluate the probability of a character of the sample under examination falling within the

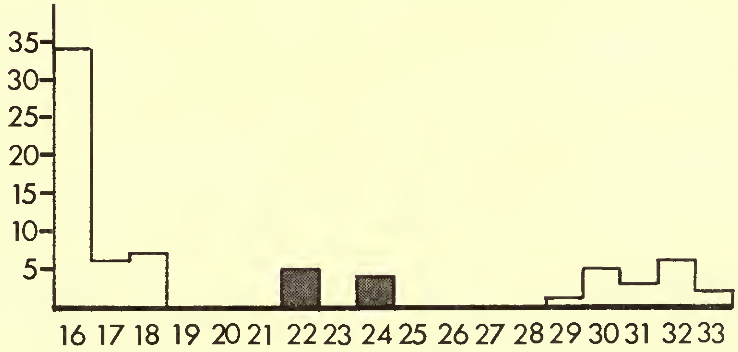

FIG. 10. A histogram of the frequencies of the lateral line scale counts in *Barbus tropidolepis* (left), the hybrids (black, centre) and *Varicorhinus tanganicae* (right).

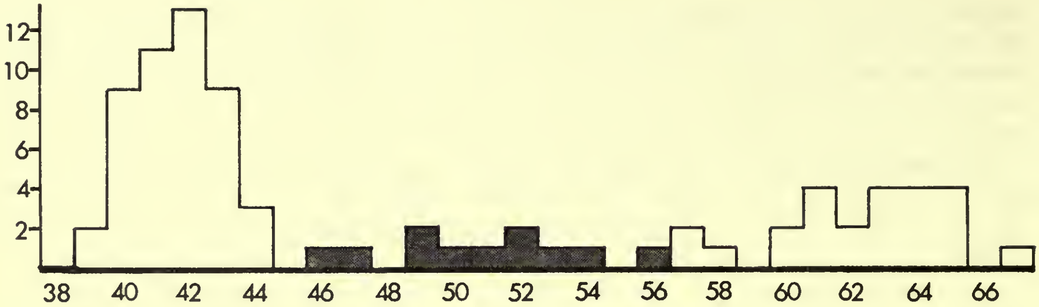

FIG. 11. A histogram of the frequencies of the scale counts around the least circumference of the caudal peduncle in *Barbus tropidolepis* (left), the hybrids (black, centre) and *Varicorhinus tanganicae* (right).

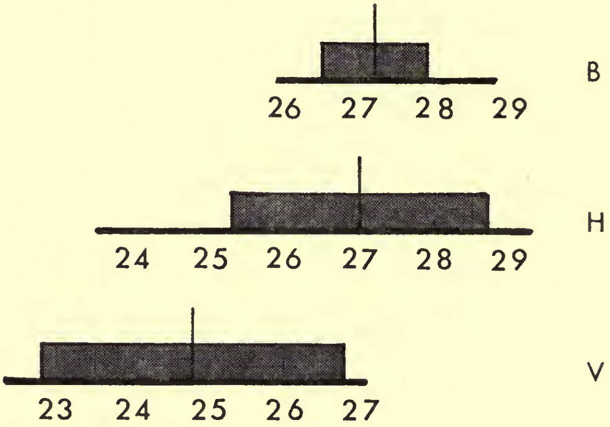

FIG. 12. A comparison of the range, mean and standard deviations of the head length in the three forms. The base line represents the range, the vertical line the mean and the black area covers one standard deviation either side of the mean. The figures are the lengths of the heads expressed as a percentage of the standard length. B = *Barbus tropidolepis*, V = *Varicorhinus tanganicae*, H = hybrids.

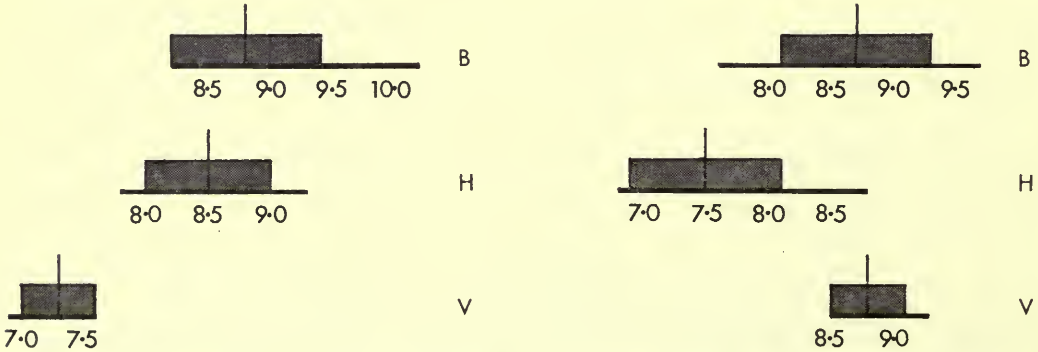

FIG. 13. Comparisons of the eye diameter (left) and interorbital width (right) in the three forms. Details as in Fig. 12.

range of that character in either of the putative parent species. The results are shown in Table 2.

TABLE 2

Character	n	$\bar{x}$	s.d.	% B	% V	P
H						
V. t.	5	24·82	2·05			0·4
Hyb.	11	26·97	1·72	91	9	
B. t.	10	27·18	0·77			0·7
I						
V. t.	5	7·30	0·30			0·1
Hyb.	11	8·54	0·55	81	19	
B. t.	10	8·83	0·61			0·25
IO						
V. t.	5	8·78	0·31			0·1
Hyb.	11	7·46	0·63	–	–	
B. t.	10	8·66	0·66			0·1
MW						
V. t.	5	8·72	0·55			0·1
Hyb.	11	6·86	0·63	52	48	
B. t.	10	5·90	0·51			0·1
Dsp						
V. t.	5	23·94	2·35			0·4
Hyb.	11	26.34	1.52	44	56	
B. t.	10	28·2	1·59			0·1
Ab						
V. t.	5	1·35	1·06			0·1
Hyb.	11	1·80	0·28	–	–	
B. t.	10					–
Pb						
V. t.	5	3·06	1·36	–	–	0·78
Hyb.	11	3·24	0·54			–
B. t.	10					

For the characters H, I, MW and Dsp the mean for the hybrid lies between the means for the other two species. The % B refers to the percentage proximity of this mean to the mean for *Barbus tropidolepis* and the % V refers to the percentage proximity to the *Varicorhinus tanganicae* mean. The probability, P, refers to the probability of observing a mean equal to the Balon specimen value if the sample had come from one of the other two species.

The morphometric measurements of the putative hybrids are satisfactorily intermediate for the characters MW and Dsp. However, the head length results are not as significant as they were for *Barbus alluaudi* (Banister, 1972). In that case the percentage likeness of the head length to each of the putative parents is

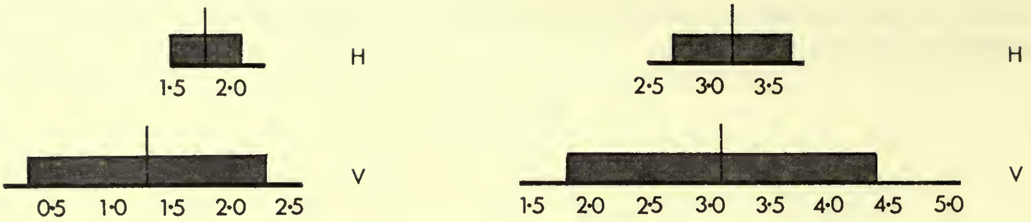

FIG. 14. Comparisons of the anterior (left) and posterior (right) barbel lengths in the three forms. Details as in Fig. 12.

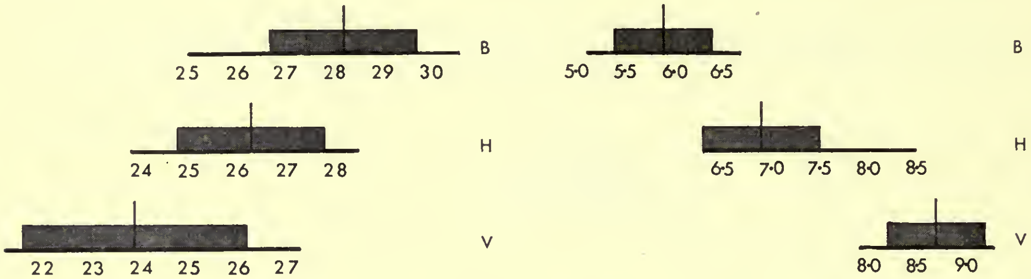

FIG. 15. Comparisons of the dorsal spine length (left) and the mouth width (right) in the three forms. Details as in Fig. 12.

69 and 31% respectively. It can be seen from Table 2 that the head-length of the Balon fish is much closer to that of *Barbus tropidolepis* than to that of *Varicorhinus tanganicae* (% B=91 ; % V=9). One striking similarity between *Barbus alluaudi* and the Balon fishes can be seen in the interorbital width. In both cases, the hybrid interorbital width is less than that of the putative parents, the latter differing but little from each other in this character.

Although generally it is true to say that African *Barbus* species have longer barbels than African *Varicorhinus* species, it is not true in this case. What little difference exists between the putative hybrids and *Varicorhinus tanganicae* shows that the hybrid has slightly longer barbels.

The results of the morphometric characters analysed in Table 1 and the characters described in the earlier part of the text indicate that it is unlikely that the Balon specimens are extreme forms of either *Barbus tropidolepis* or *Varicorhinus tanganicae.* The degree of intermediacy hints most strongly at a hybrid origin.

The evidence for the hybrid origin of the Balon fish is circumstantial and rests solely on the fact that in many characters these specimens are intermediate between *Barbus tropidolepis* and *Varicorhinus tanganicae.* This is the second example of hybridization between species of the genera *Barbus* and *Varicorhinus* in Africa. Such intergeneric hybridization raises doubts about the validity of the two genera. The mouth shape is the main character used to distinguish the two genera and yet this has been shown (Groenewald, 1958 ; Banister, 1973) to be a variable feature of little value at the generic level. Some *Barbus* species show extra-limital variation and achieve the *Varicorhinus* facies, or at least a close approximation to it. In all probability the true situation is that the genus *Varicorhinus* is polyphyletic and contains some species whose phyletic status may be best expressed by placing them in the genus *Barbus*. A full revision of the genus *Varicorhinus* is needed to clarify these anomalies. This work is in progress.

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My thanks go to Dr Eugene Balon for kindly allowing me to examine the specimens he collected. Dr P. H. Greenwood read the manuscript and offered much valuable advice. Mrs M. Clarke processed the statistical data under the guidance of Dr M. Hills. The uncredited drawings of whole fish are the work of Miss M. Holloway. The pharyngeal bones were drawn by G. Howes, who with the assistance of Mrs Clarke provided me with the radiographs.

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PLATE 1

A hybrid (top) of 133 mm SL, *Varicorhinus tanganicae* (centre) and *Barbus tropidolepis* (bottom).

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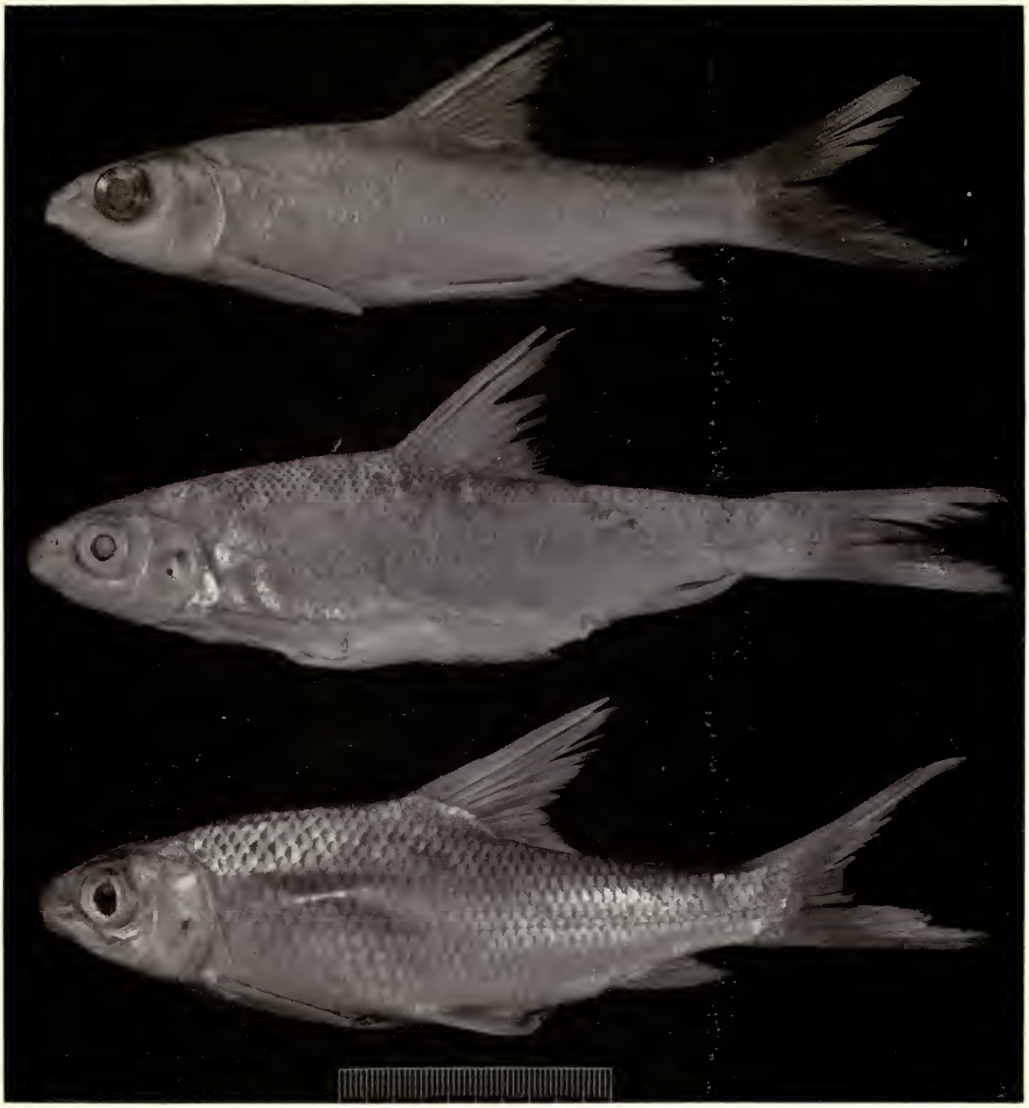
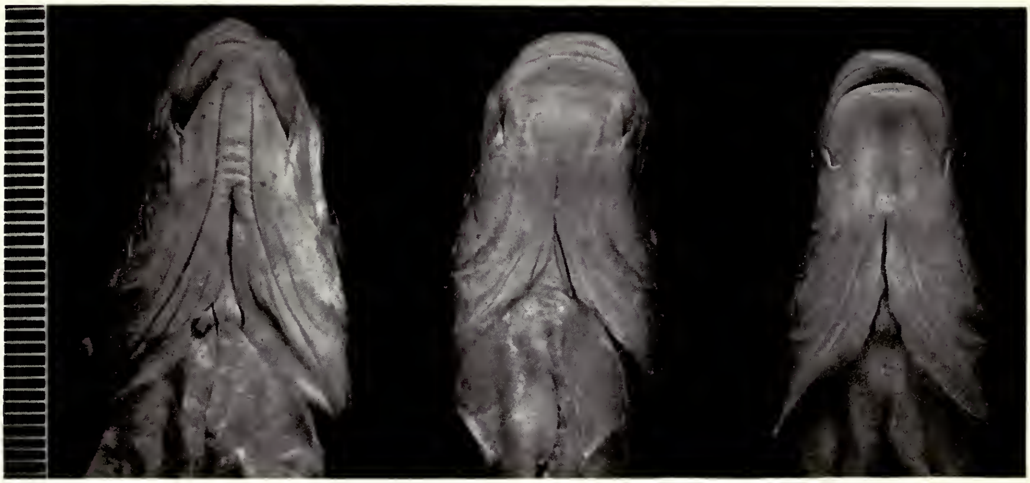


PLATE 2

Ventral views of the head of *Barbus tropidolepis* (left), *Varicorhinus tanganicae* (centre) and a hybrid of 133 mm SL (right).



TWO NEW SPECIES OF LARGE *BARBUS* (PISCES, CYPRINIDAE) FROM CENTRAL AFRICA

By K. E. BANISTER

SYNOPSIS

Two new species of large *Barbus* from central Africa are described: *Barbus huloti* from the Lake Albert basin and *Barbus humphri* from the Ituri system. *Barbus huloti* is aligned with *Barbus somereni* and *Barbus mirabilis* but the affinities of *Barbus humphri* are uncertain.

INTRODUCTION

During a recent visit to the Institute Royale des Sciences Naturelles, Brussels, I found in the collections two series of specimens labelled *Barbus altianalis* from localities in which this species was unknown. Further examination showed that each series represented a new species. The series from the Vuda River (a feeder stream of Lake Albert) is particularly interesting because it represents only the second known species of large *Barbus* from that lake basin.

Notes on counts and measurements

The standard length (SL) was taken in the usual manner. The lateral line count (LL) was taken from the first pore-bearing scale behind the head to the scale lying lateral to the end of the hypurals. The body depth (D) is the maximum body depth, usually to be found just in front of the dorsal fin. The anterior limit for the head length (H) and snout length (Snt) was the premaxillary symphysis, with the premaxillae retracted. The posterior limit for the snout is the anterior margin of the orbit and for the head length is the most posterior part of the bony edge of the operculum. The term 'mouth width' (MW) refers to the width across the lower jaw at the level of the angle of the mouth. The pectoral fin length (Pct) is the total length of the fin, measured in a straight line from the base of the first fin ray to the distal extremity of the fin. The measurements were taken in this way because of the ease of so doing with dial calipers, which were used on all fish except the smallest, when dividers were used. The caudal peduncle length (CPl) is the horizontal distance from the posterior angle of the base of the last anal ray to the end of the hypurals and the caudal peduncle depth (CPd) is the least depth of that part. The interorbital width (IO) was measured as the least distance between the bony edges of the interorbital space. The eye diameter (I) is the horizontal diameter of the visible part of the eye. Dsp symbolizes the height of the dorsal fin from the base of the first spine to the distal extremity of the longest fin ray. With any measurements which were repeatable on both sides of the fish (e.g. the anterior barbel, Ab,

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or posterior barbel, Pb) the larger was taken except in cases where a deformity was obvious.

The majority of measurements were taken to the nearest millimetre ; the exceptions were some measurements made on small fishes ; these were taken to the nearest half millimetre.

The mean is symbolized by x̄, the standard deviation by s.d., the standard error by s.e. and the number of fish in the sample by n.

DESCRIPTION OF SPECIES

Barbus huloti sp. nov.

Holotype. The holotype is a fish of 140 mm SL, no. 13289.558 in the collections of the Institute Royale des Sciences Naturelles, Brussels. Ten specimens *ex* no. 13288 are paratypes, as is BMNH.1975.4.30 :1. These fishes were collected by M. Hulot on 4 August 1953 at Zega on the Vuda River, Lake Albert (=Lake Mobuto Sese Seko) basin, Zaire, 1°44′N, 30°45′E.

Description. The description is based on 36 specimens, 68–282 mm SL.

	n	x̄	s.d.	s.e.	range
SL	–	–	–	–	68 –282 mm
D	35	28·1	1·8	0·3	25·0–33·7
H	36	27·5	1·3	0·2	22·6–29·4
I	36	6·4	0·8	0·1	4·2– 7·9
IO	36	7·8	0·7	0·1	6·6– 9·6
MW	35	6·5	0·6	0·1	5·8– 8·2
Pct	36	22·5	1·4	0·2	19·5–26·1
CPl	36	16·9	1·3	0·2	13·3–19·1
CPd	36	11·9	0·6	0·1	10·8–13·5
Snt	36	8·6	0·9	0·1	6·3–10·0
Ab	36	6·1	1·4	0·2	3·1– 8·6
Pb	36	7·3	1·1	0·2	4·8–10·2
Dsp	34	25·4	2·8	0·5	19·1–30·9
S-d	12	49·3	1·5	0·4	46·3–52·8
S-p	12	52·1	1·4	0·4	50·8–55·4

Unless stated otherwise all measurements are expressed as a percentage of the standard length.

The body is compressed and shallow with the ventral profile gently convex from the gill isthmus to the anal fin base (Fig. 1). The mouth (Pl. 1) is subterminal or ventral. The lower jaw is long with a curved buccal edge. Usually a thin mental lobe is present but in a few specimens this is greatly reduced, although the lip is always continuous. The skin of the lips, snout, base of the barbels and adjacent gular regions has a velvety texture caused by large numbers of minute papillae.

Sections were cut of the papillae but the state of preservation of the tissues was inadequate for detailed histological examination. The larger specimens (above about 120 mm SL) have tubercle scars on the skin of the cheeks. In a few of the largest fishes two rows of tubercles are present on the anal fin and small scattered

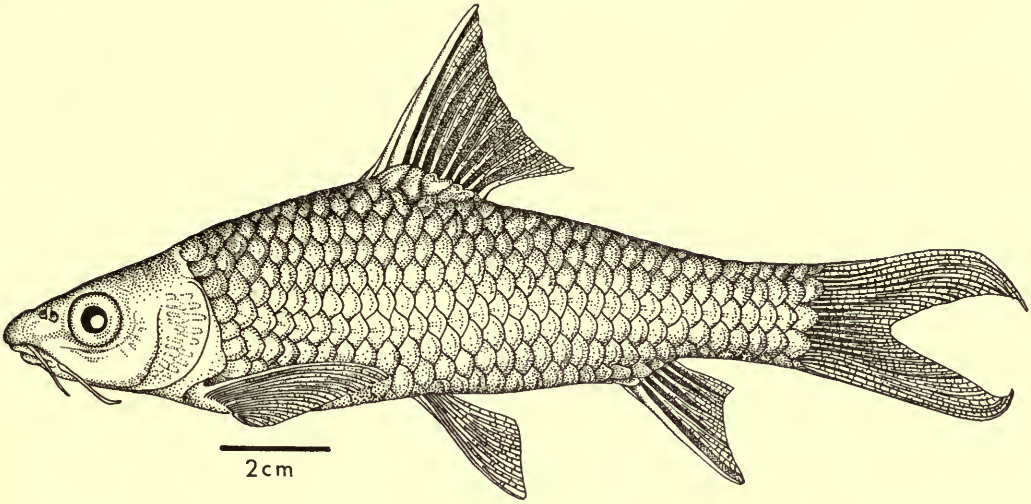

FIG. 1. *Barbus huloti*, holotype, 140 mm SL.

tubercles, or their scars, are present on the top of the head. The eyes are protuberant in most specimens but this may be a post-mortem effect of perhaps the result of the fishes having been collected by dynamiting. A few specimens (see Pl. 1) have a few poorly developed rows of pit organs on their cheeks.

The vertebrae in the twelve specimens radiographed number 18+21 (f1), 19+20 (f3), 19+21 (f4), 20+20 (f3) or 20+21 (f1). This count includes the vertebrae incorporated in the Weberian mechanism.

Dorsal fin. There are 4 unbranched rays and 8 (f7) or 9 (f29) branched rays. The last unbranched ray is thickened into a smooth, straight spine ($\bar{x}=25{\cdot}4$; s.d.$=2{\cdot}8$; s.e.$=0{\cdot}5$; range 19·1–30·9). Most specimens have a sheath of scales covering the bases of the simple rays and the first five or six branched rays. The dorsal fin origin is in advance of the pelvic fin origin.

The *anal fin* has 3 unbranched rays and 4 branched rays (f36).

Squamation. In the lateral line series there are 24 (f2), 25 (f4), 26 (f7), 27 (f11), 28 (f9) or 29 (f3) scales. From the dorsal mid-line to the lateral line there are 4½ (f6) or 5½ (f30) scales and from the lateral line to the mid-ventral line there are 4½ (f15), 5 (f1) or 5½ (f11) scales. Between the lateral line and the base of the ventral fin there are 2 (f1), 2½ (f22) or 3 (f7) scales. Scale counts are not obtainable on all specimens. There are 12 (f36) scales around the least circumference of the caudal peduncle.

The scale striations are disposed radially on the anterior scales but are parallel or slightly convergent on the posterior scales (Fig. 2).

Pharyngeal bones and teeth (Fig. 3). The pharyngeal teeth number 2.3.5–5.3.2 in all the 12 specimens examined. There is no significant change in the shape of the pharyngeal teeth with an increase in the size of the fish. The second tooth of the inner row is always mammiliform and never develops a molariform crown. The

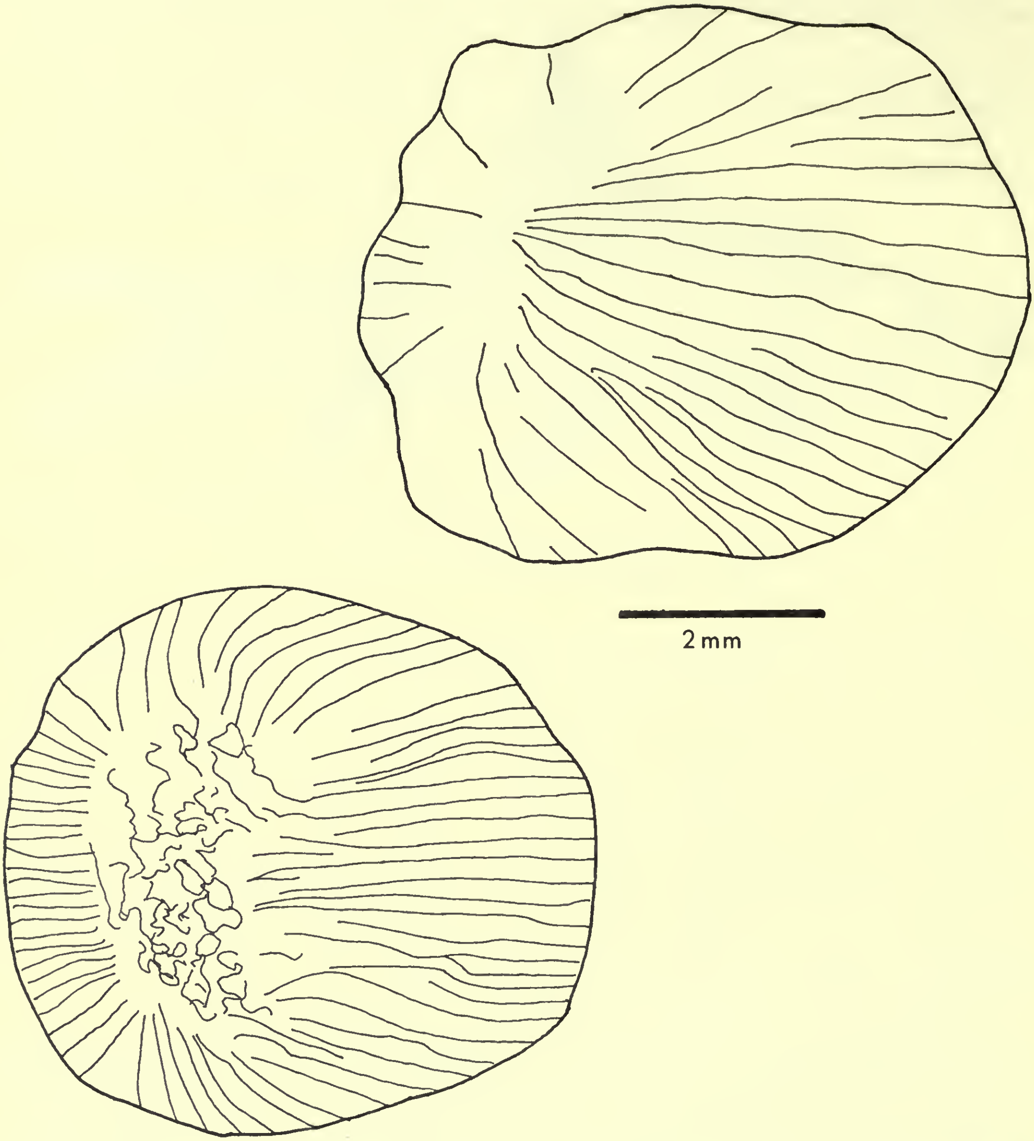

FIG. 2. *Barnus huloti*, scale striations. Above, the third scale from the row above the lateral line ; below, the fifteenth scale from the same row.

mean tip-to-tip length of the pharyngeal bones of a specimen of 164 mm SL is 17·0 mm and that of a specimen 216 mm SL is 23·5 mm.

Gill-rakers. In 12 specimens examined there are 10 (f1), 11 (f2), 12 (f3) or 13 (f6) gill-rakers on the lower limb of the first gill-arch. The gill-rakers are slightly curved and obtusely pointed.

Coloration. Alcohol-preserved specimens are dark brown dorsally and paler on the flanks and belly. The centre of each scale is lighter than the edges. Diffuse dark pigment is present in the proximal part of the membrane of all fins. The lateral line is more conspicuous on the caudal peduncle where it is paler than the background.

ETYMOLOGY. This species is named in honour of the collector, M. Hulot.

DISTRIBUTION. This species is known only from pot-holes in the bed of the Vuda River, a feeder stream of Lake Albert, 1°44′N, 30°45′E, Zaire.

DIAGNOSIS AND AFFINITIES. The only other species of large *Barbus* recorded from the Lake Albert basin is *Barbus bynni* (Banister, 1973 : 27). This nilotic

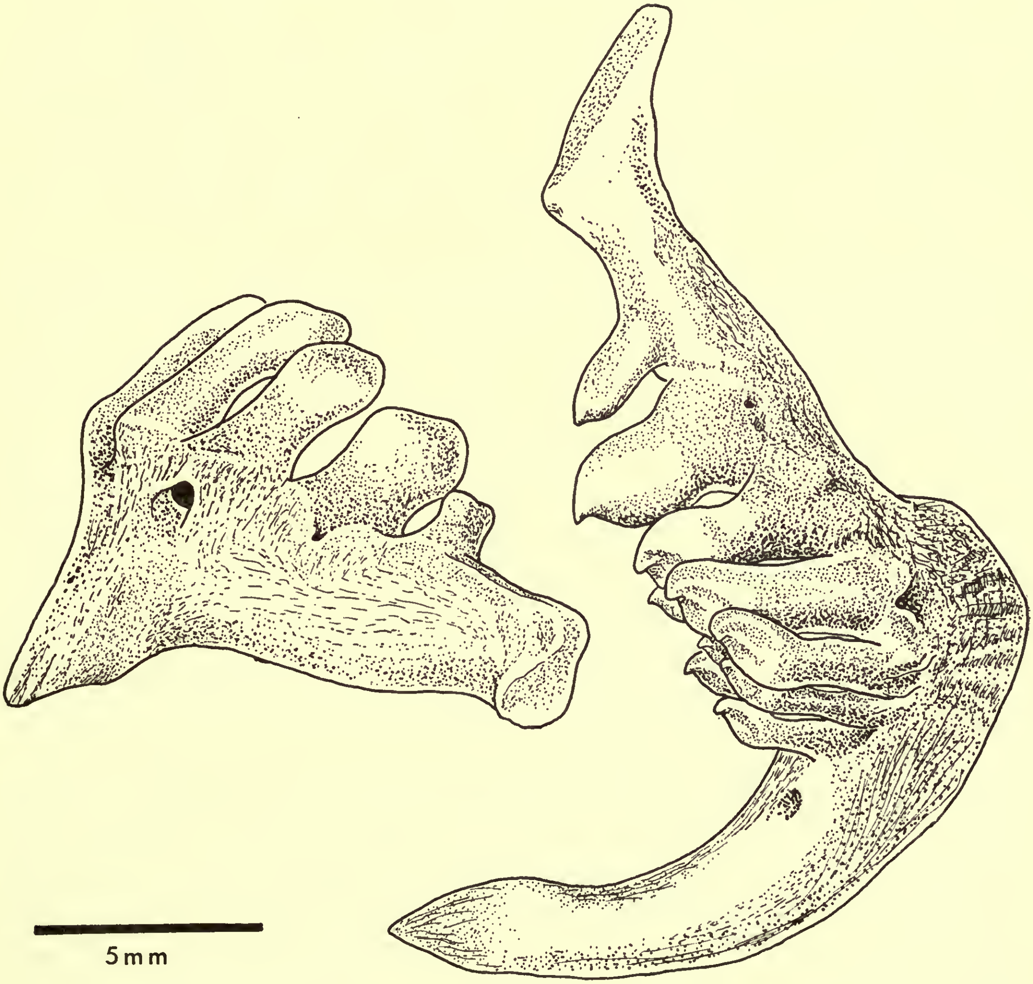

FIG. 3. *Barbus huloti* : left pharyngeal bone of the holotype.

species is, by its massive dorsal spine, deep body and parallel, sinuous striations on the scales, easily distinguished from *Barbus huloti*.

Superficially, *Barbus huloti* resembles *Barbus altianalis*, subspecies of which are found in Lake Victoria (including Lake Kyoga), Lake Kivu and Lakes Edward and George and their feeder streams. Meristic and morphometric differences between the three subspecies are small (see Banister, 1973), but meristic and morphometric data for specimens of two of the three subspecies within the size range of the *Barbus huloti* sample are given in Tables 1 and 2. The main differences between *Barbus altianalis* and *Barbus huloti* are in scale number as well as in the eye, barbel length and length of dorsal spine.

TABLE 1

Comparisons of the mean and range of certain characters in *Barbus altianalis* and *B. huloti*

	B. a. radcliffii n = 18		*B. a. eduardianus* n = 33		*B. huloti* n = 36	
	x̄	range	x̄	range	x̄	range
SL (mm)		90–282		68–280		68–282
I	7·9	5·0–10·0	8·8	6·4–11·5	6·4	4·2– 7·9
Ab	5·3	3·6– 8·6	4·2	2·2– 6·4	6·2	3·1– 8·6
Pb	6·4	4·5– 9·6	5·7	3·9– 7·7	7·3	4·8–10·2
Dsp	19·9	13·6–30·4	18·9	13·2–25·0	25·4	19·1–30·9

TABLE 2

A comparison of the number of scales in the lateral line series in *Barbus altianalis radcliffii* (B. a. r.), *B. a. eduardianus* (B. a. e.) and *B. huloti* (B. h.)

No. of scales	24	25	26	27	28	29	30	31	32	33	34	35	36
B. a. r.						1	3	5	3		4		
B. a. e.						3	6	2	6	4	4		1
B. h.	2	4	7	11	9	3							

There are, in addition, some less quantifiable differences between *Barbus huloti* and *Barbus altianalis*. The latter species has never been observed to develop tubercles, nor to have papillae around the mouth. The scale striations of *Barbus altianalis* are more or less parallel and their direction does not vary with the position of the scale on the body. The pharyngeal bones and teeth of *Barbus altianalis* vary in shape and size (with the diet), a phenomenon not yet observed in *Barbus huloti*.

An attempt to explain the absence of *Barbus altianalis* from Lake Albert was made by Banister (1973 : 22) and the arguments given there form an essential background to the current problem. The central part of this problem is to determine the likelihood of *Barbus altianalis* populations having moved from Lake Edward via the Semliki River into Lake Albert in the last 8000–10 000 years. This date coincides with the cessation of the Katwe vulcanicity (Bishop, 1969), an event contemporaneous with the fish extinctions in Lake Edward (Greenwood, 1959; Kendall, 1969). Hitherto there has been no evidence of any faunal interchange via the Semliki River since that time. This is rather puzzling, especially if the latter river is compared with the Ruzizi River.

The Ruzizi River dates, in more or less its present form, from about 13 000 B.P. (see evidence summarized in Banister, 1973) so that in each case the time scale is of the same order of magnitude. However, the slope of the two rivers is very different ; the Ruzizi drops approximately 590 m in 120 km whilst the Semliki only drops approximately 290 m in 220 km. Yet one fish, *Barilius moori* (see Poll, 1952), is known to have ascended the steeper Ruzizi River. *Barbus altianalis altianalis* has not descended the Ruzizi River into Lake Tanganyika although it has been reported from the Sange River, a tributary of the Ruzizi (Poll, 1952). A known ascent of the Ruzizi River would suggest that current speed alone is unlikely to be a barrier to migration along the gentler Semliki River. Fryer (1968) postulated that cold water flowing down the Ruwenzori mountains into the Semliki may form an effective barrier. However, Beadle (1974 : 139, 177, 181) points out that the main drop in the Semliki River bed is confined to a small distance and he thinks that it is these rapids and not the temperature that are the main barrier to the movement of fishes.

Another factor to consider is the rate of evolution of *Barbus altianalis*. It is assumed that this species was originally confined to the headwaters of the River Zaire before tectonic movements resulted in the formation of the lakes (Banister, 1973). The three subspecies have diverged but little from each other since their initial isolation. The time of their separation and isolation is in the region of 100 000 B.P. (the date of the Bufumbiro volcanoes – see Banister, 1973). Within the three subspecies there is no evidence of a potential for tachytelic evolution such that a population with *Barbus altianalis* characters would manifest *Barbus huloti* characters within 10 000 years. There is no morphological nor palaeozoogeographical evidence that indicates a sufficiently close relationship between *Barbus altianalis* and *Barbus huloti* to justify the inclusion of these species within the same supraspecific complex.

Barbus somereni Boulenger, 1911 and *Barbus mirabilis* Pappenheim & Boulenger, 1914 live in the streams of, respectively, the Ruwenzori mountains and the Ituri system. They both have scales on which the striation pattern differs with the position of the scale on the body. *Barbus huloti* displays the same phenomenon. There are certain characters present in *Barbus huloti* that are not found in the other two species ; these include papillae around the mouth, a long dorsal spine, a slender body and tubercles on the cheeks. *Barbus somereni* and *Barbus mirabilis* both have bulky bodies and a higher modal number of branched rays in the dorsal fin (9 or 10 compared with 8 or 9). The presence of variable scale striation patterns in the three species is regarded as a synapomorphic character indicating that *Barbus huloti* is more closely related to *Barbus somereni* and *Barbus mirabilis* than to Barbus *altianalis*. This character is interpreted as synapomorphic because (a) it is of infrequent occurrence and (b) it is theoretically derivable from the commoner condition of sinuous, parallel striations.

Geographically, there is nothing inconsistent in such a relationship. *Barbus somereni* lives in fast-flowing streams up to altitudes of 1750 m (Greenwood, 1966).

Barbus mirabilis comes from the Ituri River to the west of the rift valley. *Barbus huloti* is found in a fast-flowing feeder stream of Lake Albert on the floor of the rift valley. It was supposed (Banister, 1973) that *Barbus somereni* and *Barbus mirabilis* are the descendants of a once homogeneous population found in the upper reaches of the formerly more extensive Zaire system. *Barbus huloti* could, therefore, represent a segment of this population that became isolated on the floor of the rift valley.

The fishes of the Ituri system are poorly known (see below). The Ituri catchment is largely separated from the Lake Albert catchment area by the scarp wall of the rift valley. Only at the south-west part of the lake and towards the Semliki River is the scarp less severe. There the feeder streams of Lake Albert extend westwards and the relatively low watershed offers the possibility that at some time in the past there may have been movement of fishes between Lake Albert and the Ituri system. *Barbus somereni* has not, to date, been recorded from Ruwenzori streams flowing into the Semliki River.

On the available information I align *Barbus huloti* with *Barbus somereni* and *Barbus mirabilis*. Whether each species represents an isolated population of a widespread ancestral species or whether *Barbus huloti* is an evolved isolated population of one of the other two species cannot, at the moment, be determined.

Barbus humphri sp. nov.

HOLOTYPE. The holotype (Fig. 4) is a fish of 145 mm SL, no. 13289.559 in the collections of the Institute Royale des Sciences Naturelles, Brussels. Ten specimens *ex* no. 13289 are paratypes, as is BMNH.1975.4.30:2. These specimens were collected with some 500 others in the River Tabie, North Kivu district, Zaire, about 25 km south of Beni.

DESCRIPTION. The description is based on 12 specimens of 82–214 mm SL.

	x̄	s.d.	s.e.	range
SL	–	–	–	82 –214 mm
D	25·8	1·8	0·5	24·0–30·3
H	27·2	1·5	0·4	24·9–30·3
I	5·4	0·8	0·2	4·2–7·3
IO	7·8	0·6	0·2	6·9–9·0
MW	6·6	0·7	0·2	5·9–7·8
Pct	19·4	1·3	0·4	17·3–22·1
CPl	16·2	1·3	0·4	13·4–18·2
CPd	10·8	0·4	0·1	9·7–11·3
Snt	8·7	0·5	0·1	7·9–9·5
Ab	6·9	1·3	0·4	4·7–8·8
Pb	7·8	0·9	0·3	6·1–9·2
Dsp	22·9	1·8	0·9	15·9–28·0
S-d	46·8	1·8	0·5	44·9–50·7
S-p	51·1	1·8	0·5	48·3–54·0

Unless stated otherwise all measurements are expressed as a percentage of the standard length.

The body is shallow, thick and terete. Almost all the specimens have a conspicuous coating of mucus. The snout is blunt with, in larger fishes, a few very

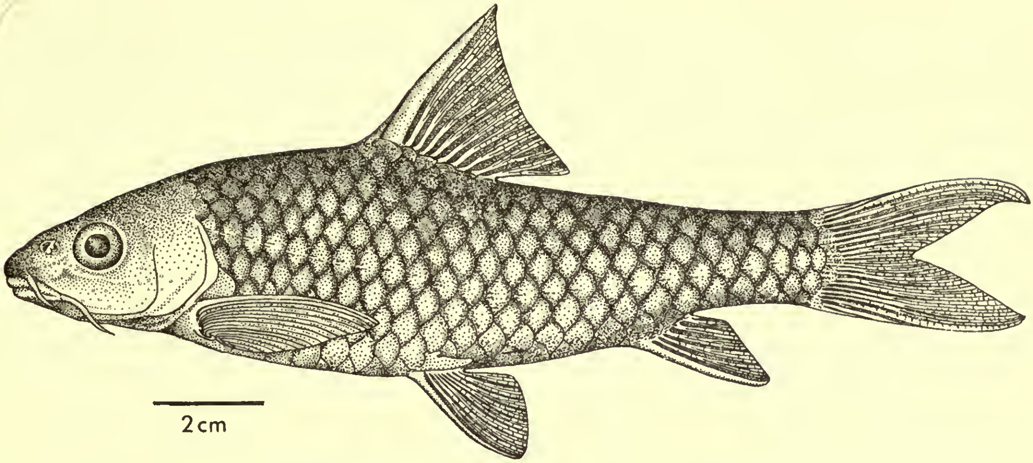

FIG. 4. *Barbus humphri*, holotype, 145 mm SL.

small tubercles on its lateral faces. The horseshoe-shaped mouth is subterminal and has an uninterrupted lower lip. A small mental lobe is occasionally present. The vertebrae in 12 specimens radiographed number 18+21 (f1), 19+19 (f2), 19+20 (f2), 19+21 (f2), 20+19 (f2), 21+18 (f2) or 21+19 (1).

Dorsal fin. There are 4 simple rays (f12), the last of these a stout, rather blunt spine, sometimes shorter than the longest branched rays. A raised sheath of scales is always present at the base of the simple rays, and in a few specimens it extends posteriorly to about the mid-point of the fin. There are 9 (f12) branched rays. The dorsal fin is in front of the pelvic fin origin.

Squamation. In the lateral line series there are 22 (f4), 23 (f3), 24 (f4) or 25 (f1) scales. There are 4½ (f12) scale rows between the dorsal mid-line and the lateral line. Between the lateral line and the ventral mid-line there are 4½ (f12) scale rows. From the lateral line to the base of the pelvic fin there are 2½ (f12) scale rows. There are 12 (f12) scales around the least circumference of the caudal peduncle. The scales bear parallel striations (Fig. 5).

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2 in the 12 specimens examined. The first tooth (Fig. 6) of the inner row is small and compressed, i.e. longer than wide (length taken in the plane of the anterior edentulous process, width horizontally at 90° to that plane). The second tooth is also compressed, little enlarged and with a mamilliform crown. The third, fourth and fifth teeth approach a circular cross-section and become progressively more recurved. The teeth of the second and third rows resemble the posterior teeth of the inner row. The mean tip-to-tip measurement of the pharyngeal bones of a fish of 165 mm SL is 12·8 mm and that of a specimen of 214 mm SL is 19·2 mm.

Gill-rakers. In the 12 specimens examined there are 10 (f3), 11 (f8) or 12 (f1) gill-rakers on the lower limb of the first gill-arch. The gill-rakers are scimitar shaped with small conical processes on the leading edge.

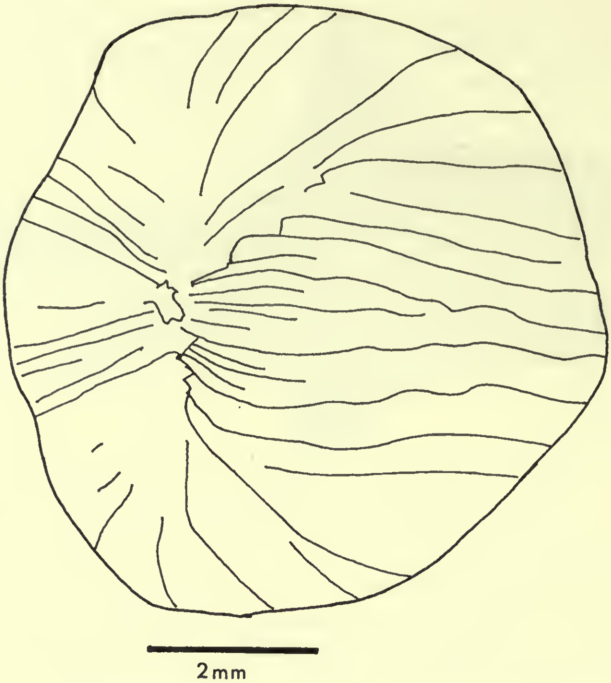

FIG. 5. *Barbus humphri* : fifth scale from the row above the lateral line of a specimen of 145 mm SL.

Coloration. Alcohol-preserved specimens are dark brown above, paler beneath. The scales on the flanks are dark edged. Traces of dark pigment remain on the pelvic, pectoral and anal fins.

ETYMOLOGY. This species is named in honour of Dr P. Humphry Greenwood for his services to African ichthyology.

DISTRIBUTION. This species is known only from the type locality, the River Tabie about 25 km south of Beni, North Kivu district, Zaire.

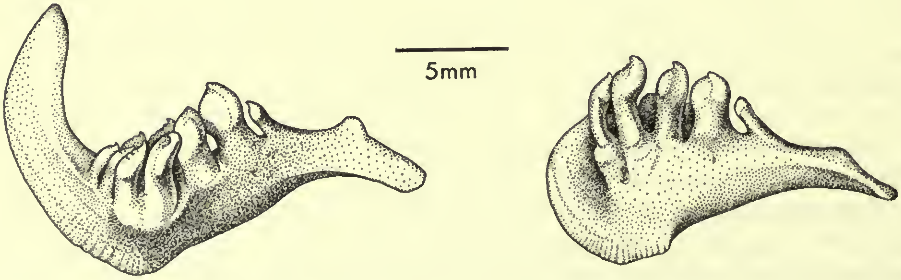

FIG. 6. *Barbus humphri* : left pharyngeal bone.

Diagnosis and affinities. The large *Barbus* species of the head waters of the Zaire system are poorly known, especially in the Ituri region. Only four species, *Barbus fasolt* Pappenheim, *Barbus mawambi* Pappenheim, *Barbus mirabilis* Pappenheim & Boulenger, and *Barbus mawambiensis* Steindachner, are recorded from the Ituri region. *Barbus paucisquamatus* Pellegrin and *Barbus longifilis* Pellegrin are known from rivers in the Lowa system to the west of Lake Kivu (and to the south of the Ituri system).

The outstanding feature of *Barbus humphri* is the low number of lateral line scales. *Barbus fasolt* can also be easily distinguished from *Barbus humphri* because it has a flexible last simple ray in the dorsal fin. *Barbus mawambi* has more scales in the lateral line series (29 *fide* Pappenheim & Boulenger, 1914 ; cf. 22–25 in *B. humphri*) and 10 branched rays in the dorsal fin (cf. 9). *Barbus mirabilis* is a bulky-bodied fish with 28 scales in the lateral line series and a variable pattern of striations on the scales (see p. 197).

Barbus mawambiensis, the only other species recorded from the Ituri system, presents a problem. This species was described as *Barbus hindii* var. *mawambiensis* by Steindachner (1911) on the basis of seven, now untraceable, specimens. His description, as well as his determination of this form as a variety of *Barbus hindii*, draws attention to the superficial resemblance between these specimens and *Barbus hindii* (=*Barbus oxyrhynchus*) from the Athi–Tana system in East Africa. The differences given by Steindachner between *Barbus hindii* var. *mawambiensis* and *Barbus hindii* are a deeper caudal peduncle in the former (Cpl/Cpd 1·0–1·9 ; cf. 1·5–1·67) and more (*sic*) scales in the lateral line (21–24) than in *Barbus hindii*. (Boulenger, 1902, gives 25–29 scales in *Barbus hindii*.) This is perplexing information, since the range of the Cpl/Cpd ratios for the four syntypes of *Barbus hindii* was quoted by Boulenger (1902) as $1\frac{1}{3}$–$1\frac{2}{3}$, while my own measurements give a mean of 1·38. The mean Cpl/Cpd ratio for all the *Barbus oxrhynchus* specimens used in an earlier study (n=108) was 1·32 (Banister, 1973). The syntypes of *Barbus hindii* have 25 (f2) or 26 (f2) scales in the lateral line series ; the range for *Barbus oxyrhynchus* is 21–28 scales : 21 (f1), 22 (f10), 23 (f15), 24 (f36), 25 (f30), 26 (f8), 27 (f6) or 28 (f1). Unfortunately, the types of *Barbus hindii* var. *mawambiensis* are untraceable, which prevents the corroboration of Steindachner's data. The specimens were deposited in the Vienna Museum, but a recent search by the curator, Dr Kähsbauer, and myself failed to find them.

In 1912 Steindachner redescribed *Barbus hindii* var. *mawambiensis* as *Barbus mawanbiensis* based on a sample of fish from the Ja River, Cameroon. The spelling (*mawanbiensis*) for the specific name must be regarded as a misprint for *mawambiensis* There are inconsistencies between his 1911 and 1912 accounts, e.g. in 1912 he states that there are fewer scales in the lateral line series of *Barbus mawambiensis* than in *Barbus hindii* – the reverse, but correct, interpretation of the 1911 information. It is, of course, possible that Steindachner muddled scale size with scale number. He does not give the size, nor the number of the specimens examined, merely their locality – the Ja River, Cameroon.

In 1914 Steindachner published another paper on a collection of fishes from the Ja River. Included in this is a further description of *Barbus mawambiensis* based on (in translation) 'three small examples from the Ja River, via Dr Haberer and from the Ituri via Herr Grauer'. The confusion is further increased by the statement that the largest of the three fishes is illustrated, although the scale on the figure shows that the smallest of the three fish is figured. (Boulenger, 1916, rightly pointed out that on Steindachner's pl. 3, figs 1 and 3 have been transposed.) Tables of measurements for each of the three specimens are given but which specimen or specimens was or were from the Ja River, and which from the Ituri, is not stated. The Ja and Ituri rivers are both in the Zaire system and are tributaries of respectively the Sangha and Aruwimi rivers which flow into the north side of the Zaire some 1000 km apart. Generally, the large *Barbus* spp. are found in the upper reaches of the tributaries, not in the main stream (pers. obs.). The two localities are some 1600 km distant and are separated by a wide sluggish river with few favourable habitats for large *Barbus* spp. Trewavas (1974 : 344) comments that the fauna of the Ja River has much in common with the rivers of Cameroon (therefore not with the Zaire system) and is also of the opinion that Steindachner's *Barbus mawambiensis* from the Ja resemble *Barbus batesii*. Although it is not known which of Steindachner's specimens came from which locality (see above), I agree with Trewavas that the *Barbus* spp. from the Ja are more likely to be related to those of west Africa (e.g. *Barbus batesii*) than to those of central Africa.

Thys van den Audenaerde (1966 : 90) compared the fauna of the upper Ja (above Molundu) with that of the Nyong River and from the faunistic and geographical evidence concluded that the upper part of the Ja had been captured by the Sangha from the upper part of the Nyong. He describes the fauna below Molundu as typically central congolese (= Zairoise). The only information given by Steindachner is that his specimens came from the Molundu district.

It would seem that the presence of the same species of large *Barbus* in the Ituri and Ja rivers is most unlikely and would present some zoogeographical enigmas.

The concept of *Barbus mawambiensis* as based on the points of agreement in Steindachner's three descriptions seems to indicate that there is a species of fish in the Ituri River which superficially resembles *Barbus hindii* but has a low number of lateral line scales. There are two specimens in the collections of the British Museum, nos. 1944.12.4:2–3 collected by Ricardo and Owen in the Epulu River (Ituri system) which have these characters and have been identified as *Barbus mawambiensis*. If this determination is correct then they can be distinguished from *Barbus humphri* by a stronger dorsal spine and a much deeper, more compressed body. These two fish also closely resemble Steindachner's figured specimen. However, the identification of these two fishes must remain tentative until the syntypes of *Barbus mawambiensis* are found.

At the moment I can find no close relatives to *Barbus humphri*; further collections from the Ituri may help to settle its relationships.

ACKNOWLEDGEMENTS

I am most grateful to M. J. P. Gosse of the Institute Royale des Sciences Naturelles in Brussels for drawing my attention to these fishes and for giving me the opportunity to examine them. Valuable comments on the manuscript were provided by Drs P. H. Greenwood and P. J. P. Whitehead. Mrs M. Clarke assisted most efficiently with the calculations. The drawings are the work of Miss M. Holloway and Mr G. Howes.

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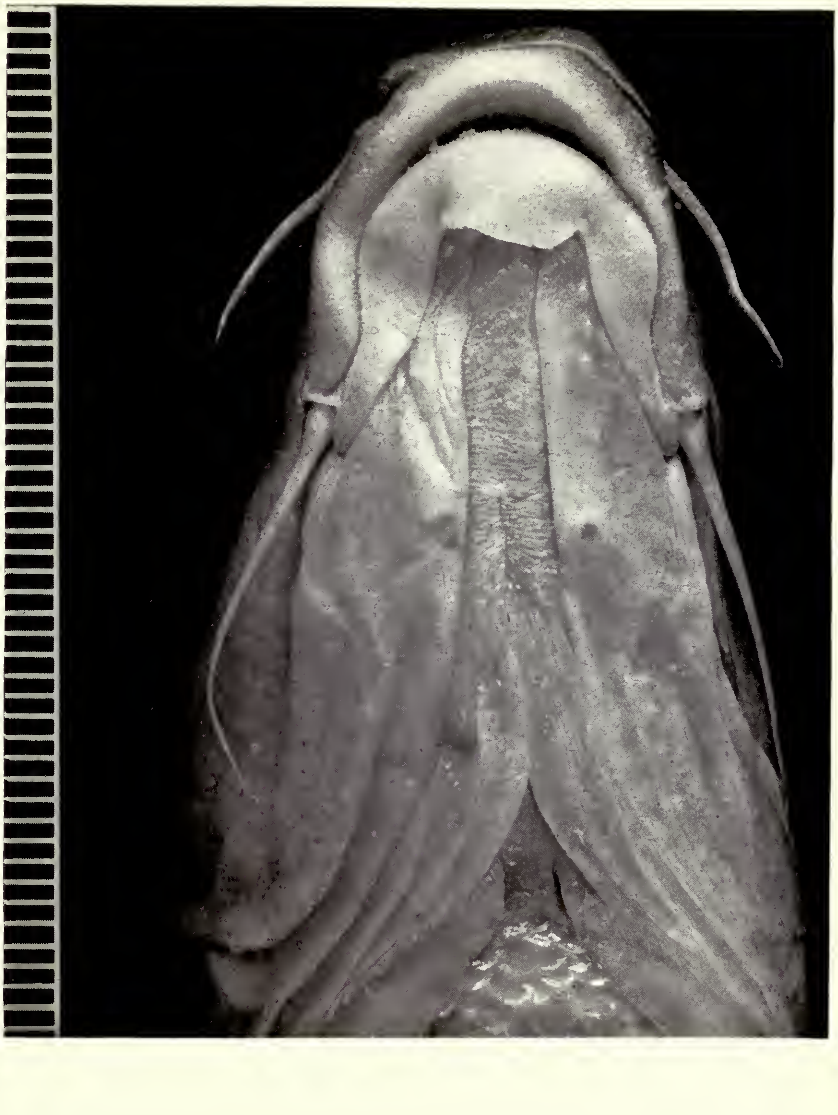
PLATE 1

Barbus huloti : ventral view of the head of a specimen of 214 mm SL to show the mouth, the papillae and the pit lines on the cheeks.



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A NEW GENUS AND TWO NEW SPECIES OF COPEPOD PARASITIC ON FRESHWATER FISHES

By G. A. BOXSHALL

INTRODUCTION

THE distribution of known species of lernaeid parasites of freshwater fishes in the Old World is notably patchy, with the majority of species known either from Africa or from eastern Asia. Between these two foci, in the region extending from India to the Mediterranean Sea, relatively few species have been recorded. It is probable that this paucity merely reflects the lack of fieldwork in this region ; thus the discovery of two new species, one from Iraq and the other from India, belonging to a new genus of lernaeid comes as no surprise.

DESCRIPTION OF NEW GENUS AND SPECIES

PSEUDOLAMPROGLENA gen. nov.

DIAGNOSIS. Lernaeidae. First pedigerous somite partially incorporated into cephalothorax. Second to fourth pedigerous somites distinct, each subdivided into anterior and posterior portions by a transverse groove. Genital complex comprising fused fifth pedigerous somite and genital somite. Genital apertures on dorsal surface of genital complex. Maxilla 2-segmented, inflated distal segment bearing single claw medially. Maxilliped small, flattened and lying in groove posterior and lateral to maxilla; 3-segmented with terminal segment bearing weak setiform spine(s) medially. Maxilliped bases connected by fleshy ridge. Thoracic legs 1–4 biramous, with 3-segmented exopod and 2-segmented endopod. Leg 5 a simple lobe with 2 apical setae. Parasitic on gills of freshwater teleosts. Male unknown.

Type species *P. annulata* sp. nov.

Pseudolamproglena annulata sp. nov.

(Figs 1a–g, 2a–e)

DIAGNOSIS. Body cylindrical and distinctly segmented (Fig. 1a, b). Cephalothorax broad, dorsal surface concave in holotype, comprising 20–25% of total body length. Anterior portion of first pedigerous somite incorporated into cephalothorax ; posterior portion free, rounded dorsally and narrower than both cephalothorax and second pedigerous somite. Second to fourth pedigerous somites separated by intersegmental sutures and subdivided into anterior and posterior portions by a transverse groove. Thoracic legs located anterior to groove. Thoracic somites increasing in size posteriorly. Genital complex small, narrower than fourth

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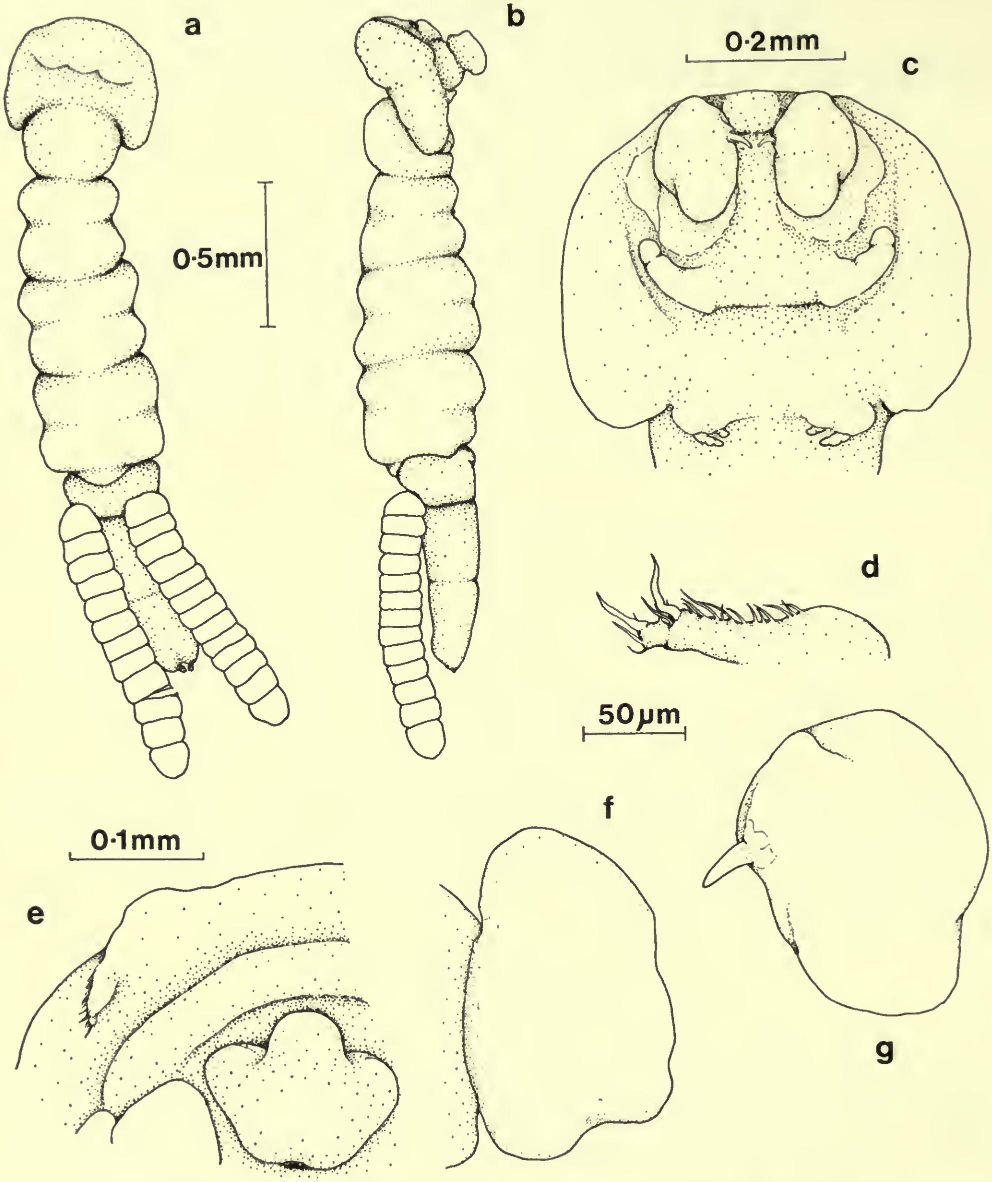
a
b
0·5mm
0·2mm
c
d
50µm
f
0·1mm
e
g

FIG. 1. *Pseudolamproglena annulata* sp. nov. female: (a) dorsal entire; (b) lateral entire; (c) cephalothorax, postero-ventral; (d) antennule, ventral; (e) oral region, ventral; (f) maxilla, lateral; (g) maxilla, ventral. Bar scale: a, b, 0·5 mm; c, 0·2 mm; e, 0·1 mm; d, f, g, 50 µm.

pedigerous somite and with genital apertures situated dorso-laterally. Abdomen elongate, consisting of 2 indistinctly divided somites. Posterior margin of anal somite bilobed bearing medially directed furcal rami. Total body length from 1·74 to 2·20 mm, with a mean of 1·97 mm (based on 2 specimens).

Egg strings uniseriate, containing up to 14 eggs. Eggs maturing in oviduct visible through body wall of second to fourth pedigerous somites.

Antennule (Fig. 1d) situated on ventral surface near anterior margin of cephalothorax, directed postero-laterally. Segmentation obscure with only the apical segment clearly delimited. Armature comprising 14 setae on anterior margin of proximal segment, 4 setae on distal segment and 2 aesthetasc-like structures, one on each segment. Antenna apparently absent.

Oral region occupied by large trilobed structure (Fig. 1e), probably representing the labrum, anterior to which lies a transverse ridge. Maxillule absent. Maxilla (Fig. 1f, g) 2-segmented, proximal segment providing a broad base for swollen, gobular distal segment. Entire surface of distal segment ornamented with minute tubercles. Single, dorsally curved spine present on medial surface of segment. Maxilliped inconspicuous, dorso-ventrally flattened and lying in a groove in cephalothorax (Fig. 1c, 2a). Indistinctly 3-segmented with a broad base, elongated middle segment and subquadrate terminal segment; single setiform spine located on medial surface. Maxilliped bases connected by ridge of tissue.

Thoracic legs 1–4 (Fig. 2b, c) similar, biramous. Sympod projecting from body surface, bearing single seta lateral to exopod base. Endopod indistinctly 2-segmented, exopod 3-segmented. Leg 1 armature comprising 2 unequal setae at tip endopod, 2 at tip exopod and 1 lateral spine on basal segment of exopod. Legs 2–4 unarmed apart from 1 lateral spine on basal segment of exopod. Leg 5 (Fig. 2e) a simple process with 2 apical setae.

Furcal ramus bearing 4 setae (Fig. 2d); 1 on lateral margin, 1 on medial margin and 1 at each posterior corner. Two small papillae present on distal margin.

ETYMOLOGY. The generic name proposed indicates a close affinity to the genus *Lamproglena* Nordmann. The specific name alludes to the very distinct segmentation in this species.

MATERIAL EXAMINED. Type material 2 ovigerous ♀♀. Holotype ♀ reg. no. 1975.800; paratype reg. no. 1975.801 deposited in the collections of the British Museum (Natural History). The material was obtained from the gills of *Cyprinion macrostomus* (caught in the river Tigris at Mosul, Iraq) present in the British Museum (Natural History) collections. Additional material: 5 ♀♀, all either damaged or incomplete, collected by Mr Z. I. Fattohy from the gills of *C. macrostomus* from the same locality. Three of these specimens donated to the British Museum (Natural History) by Mr Fattohy and Dr M. H. Kasim (Mosul University).

Pseudolamproglena simplex sp. nov.
(Figs 2f–i, 3a–d)

DIAGNOSIS. Body segmentation and tagmosis as in *P. annulata* but less distinct and without intersegmental sutures between the pedigerous somites (Fig. 2f, g).

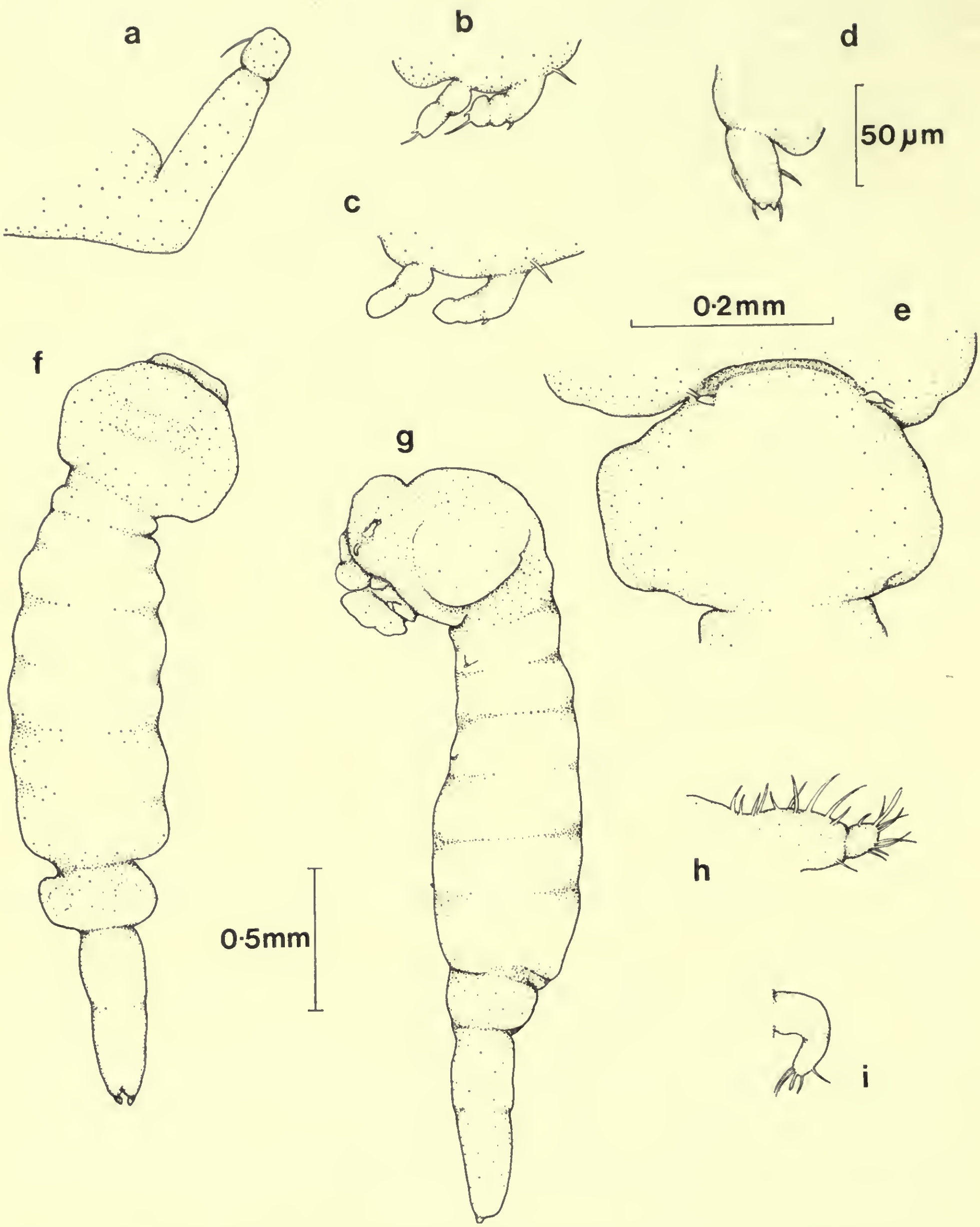

FIG. 2. *Pseudolamproglena annulata* sp. nov. female : (a) maxilliped, ventral ; (b) leg 1, ventral ; (c) leg 4, ventral ; (d) furcal ramus, ventral ; (e) genital complex, ventral. *Pseudolamproglena simplex* sp. nov. female : (f) dorsal entire ; (g) lateral entire ; (h) antennule, ventral ; (i) antenna, lateral. Bar scale : a–d, h, i, 50 µm ; e, 0·2 mm ; f, g, 0·5 mm.

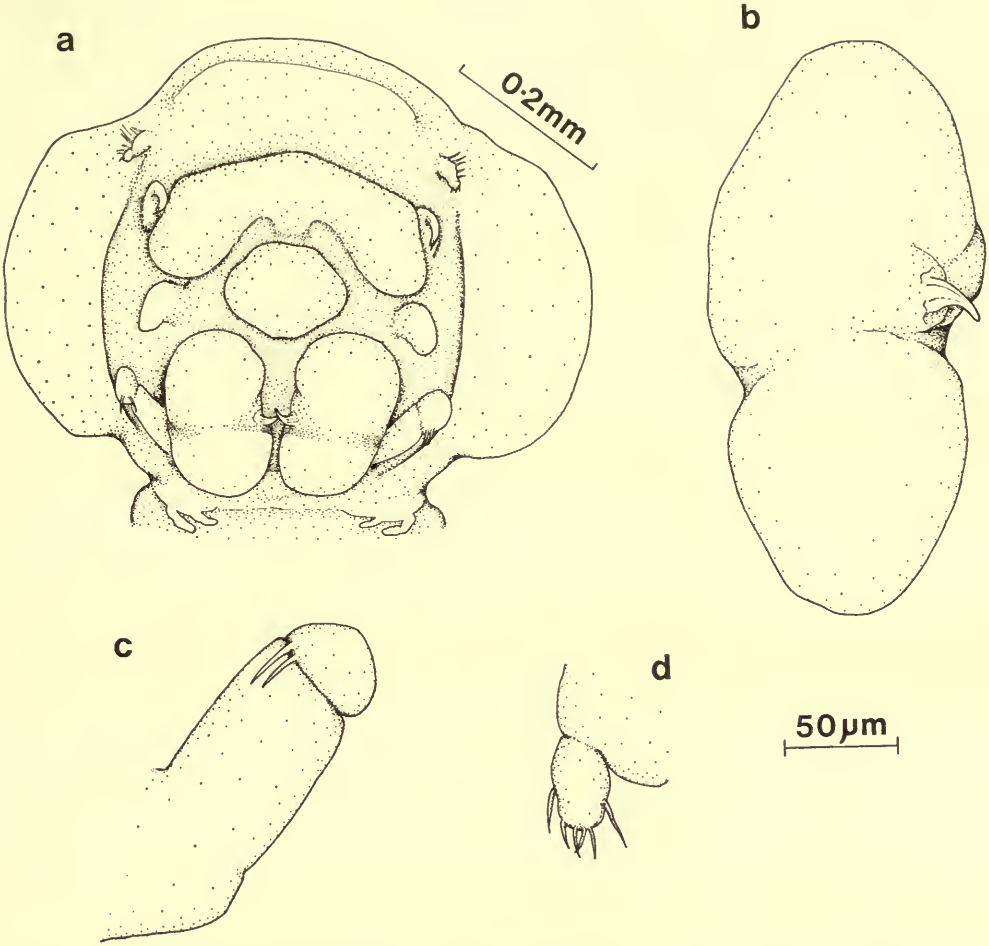

FIG. 3. *Pseudolamproglena simplex* sp. nov. female: (a) cephalothorax, ventral; (b) maxilla, ventral; (c) maxilliped, ventral; (d) furcal ramus, ventral. Bar scale: a, 0·2 mm; b–d, 50 µm.

Cephalothorax comprising about 20% of total body length. Cephalothorax with prominent anterior ridge visible from the dorsal aspect. Second to fourth pedigerous somites similar in width. Genital complex of holotype (a gravid female) with conspicuous dorsal swellings marking the genital apertures. Total body length from 1·93 to 2·45 mm, with a mean of 2·25 mm (based on 5 specimens).

Only 1 specimen ovigerous, egg string containing 20 eggs. Mature eggs in oviduct visible in second to fourth pedigerous somites.

Position of all cephalic appendages illustrated in Fig. 3a. Antennule 2-segmented (Fig. 2h); large basal segment bearing 10 setae on anterior margin and 1 on posterior margin, apical segment armed with 8 setae and an aesthetasc-like structure. Antenna (Fig. 2i) curved posteriorly, indistinctly 2-segmented and carrying an apical armature of about 5 setae.

Oral region occupied by simple hemispherical lobe, probably representing the labrum (Fig. 3a). Transverse ridge present on ventral surface anterior to labrum. Maxillule (Fig. 3a) an unarmed fleshy process situated lateral to labrum. Maxilla 2-segmented with broad basal segment and massive, inflated distal segment. Distal segment (Fig. 3b) marked by transverse constriction and armed with single curved spine on medial surface. Maxilliped indistinctly 3-segmented (Fig. 3c). Basal segments of maxilliped pair connected by transverse ridge on ventral surface. Middle segment elongate, cylindrical. Terminal segment armed with 2 basal setae on postero-medial surface.

Thoracic legs 1–4 similar to those of *P. annulata* both in segmentation and armature. Leg 5 positioned anteriorly on ventral surface of genital complex, comprising a simple process bearing 2 apical setae.

Furcal rami (Fig. 3f) armed with 6 marginal setae ; 1 lateral, 1 medial and 4 distal.

Etymology. The specific name refers to the simple, hemispherical structure of the lobe in the oral region.

Material examined. 6♀♀ (1 ovigerous). Holotype ♀ reg. no. 1975.803 ; 5 paratypes reg. nos 1975.804–808. deposited in the collections of the British Museum (Natural History). All specimens collected by Mr M. K. Jyoti from the gills of *Labeo diplostomus* caught in Dal Lake, Kashmir, India.

HOST–PARASITE RELATIONSHIPS

The two attached *P. annulata* observed were located on the anterior surface of the posterior hemibranch of gills 2 and 3. A single primary gill filament had been grasped between the maxillae and secured by the insertion of the spines. *P. simplex* attaches to the host in an identical manner but nearer to the distal tip of the gill filament than *P. annulata*. In both species the maxilla appears to be the only attachment organ and the massive development of this limb presumably compensates for the reduction of the maxilliped.

The host tissue response to the presence of the parasite was negligible in *P. simplex* infections. Different degrees of epithelial hypertrophy were observed associated with the two specimens of *P. annulata*, with a localized, minor response in one case and, in the other, a massive response which resulted in the parasite being completely enclosed by host tissue to the level of the genital complex. It has been suggested (Sproston *et al.*, 1950) that envelopment of the parasite provides additional security to the attachment of the parasite.

REMARKS

The new genus can be readily assigned to the subfamily Lamprogleninae of the family Lernaeidae. Of the two other genera in this subfamily, *Lamproglena* Nordmann and *Lamproglenoides* Fryer, the new genus is more closely allied to the former. Although the genus *Lamproglena* comprises a quite heterogeneous group of species the two new species could not be included within this genus without an unacceptable broadening of the generic diagnosis. The genus *Pseudolamproglena* is erected to contain these two species which form a well-defined group distinguishable from species of *Lamproglena* by the structure and armature of the maxillae and maxillipeds and by their distinctive somitic segmentation.

Fryer (1968) recognized several evolutionary trends within the Lernaeidae. Amongst these are the suppression of external signs of segmentation and tagmosis, the development of a 'neck', reduction of antennules and antennae and the reduction of the number of terminal spines on the maxilliped. *Pseudolamproglena* exhibits a mosaic of primitive and advanced characters with respect to these trends. It retains a primitive degree of external somitic segmentation and tagmosis combined with the specialized condition of the maxilla and maxilliped and, in *P. annulata*, with the apparent absence of the antenna. This combination of characters suggests that *Pseudolamproglena* diverged from the ancestral *Lamproglena*-like stock at an early date and that specialized adaptations of the mouthparts evolved independently.

ACKNOWLEDGEMENTS

I would like to thank Dr G. Fryer for his valuable comments on some of these specimens and Dr R. J. Lincoln for his criticism of the manuscript. I am grateful to Mr Z. Fattohy and Dr M. H. Kasim (Mosul University, Iraq) whose donation first brought *P. annulata* to my attention.

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A NEW SPECIES OF *CHONOPELTIS* (CRUSTACEA: BRANCHIURA) FROM SOUTHERN AFRICA

By G. A. BOXSHALL

INTRODUCTION

THE genus *Chonopeltis* Thiele, 1901 is endemic to Africa and comprises seven known species. The southernmost record of this genus is that of *C. meridionalis* Fryer from the Limpopo river system in Rhodesia (Fryer, 1968). It was interesting, therefore, to discover some specimens of *Chonopeltis* in a collection of crustaceans parasitic on freshwater fishes of the Orange river system. The specimens represent a new species which is described below.

DESCRIPTION OF NEW SPECIES

Chonopeltis australis sp. nov.

DIAGNOSIS. With characters of genus. Female body squat, with 2 longitudinal bands of pigment spots on thorax. Second maxilla with scale-covered prominence on proximal portion. Leg 3 less than twice as long as leg 4. Male lacking posterior projections on leg 2 sympod and lacking process on exopod of leg 4.

DESCRIPTION. *Adult female.* General appearance squat (Figs 1a, 2a), large trifoliate carapace comprising about 54% of total body length. Lateral lobes of carapace extending posteriorly to cover the bases of leg 2; oval respiratory areas on ventral surface of each lateral lobe similar to other species of genus. Chitinous supporting rods present in anterior lobe of carapace. Eyes small; ocellus small, distance between ocellus and eyes equal to interocular distance. Segmentation of thorax distinct. Two longitudinal bands of dark pigment spots present on thorax, dorsal to uteri. Abdomen comprising 20–24% of total body length. Furcal rami minute. Spermathecae short, extending to level of bifurcation of abdomen in some specimens.

First antenna (Fig. 2e) slender, indistinctly 5-segmented; apical segment bearing 3 spines. Mandible (Fig. 2b) curved, bearing 3–4 rows of denticles on convex surface and a row of spinules on concave margin. Suckers (first maxillae) as in other species of the genus. Second maxillae (Fig. 2d) with a 2-segmented proximal portion and 3-segmented distal portion; scale-covered prominence present on posterior surface near apex of second segment opposing a small elevated region on third segment; 2 small claws situated in depression at tip of terminal segment. Legs 1–4 biramous; sympod and both rami armed with single rows of setae; legs 1–3 similar in size, leg 4 about two-thirds as large as leg 3. Natatory lobes of leg 4 (Fig. 2c) extensive, meeting at ventral midline, with spinules present on posterior and medial margins.

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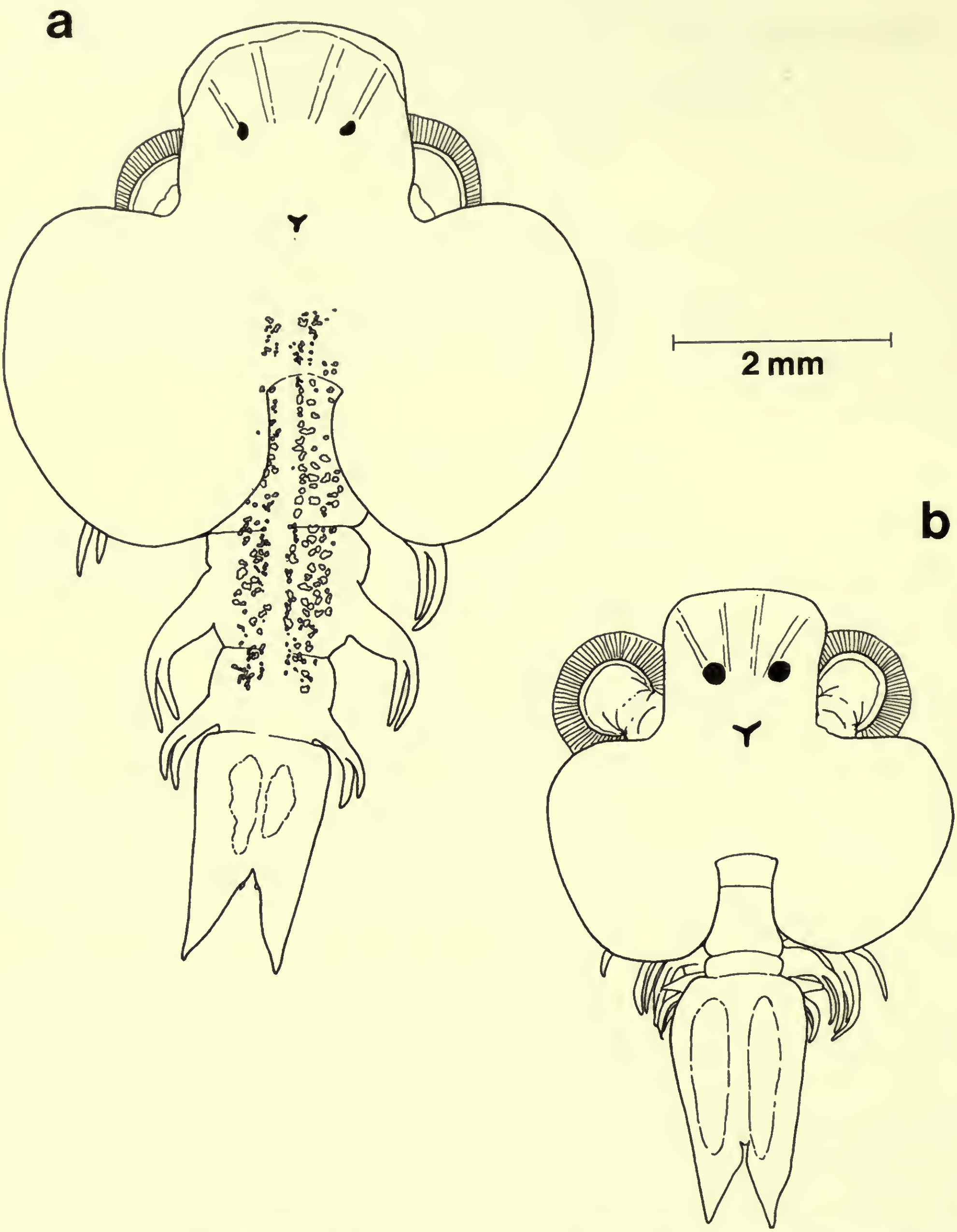

FIG. 1. *Chonopeltis australis* sp. nov. : (a) adult female, dorsal ; (b) adult male, dorsal.

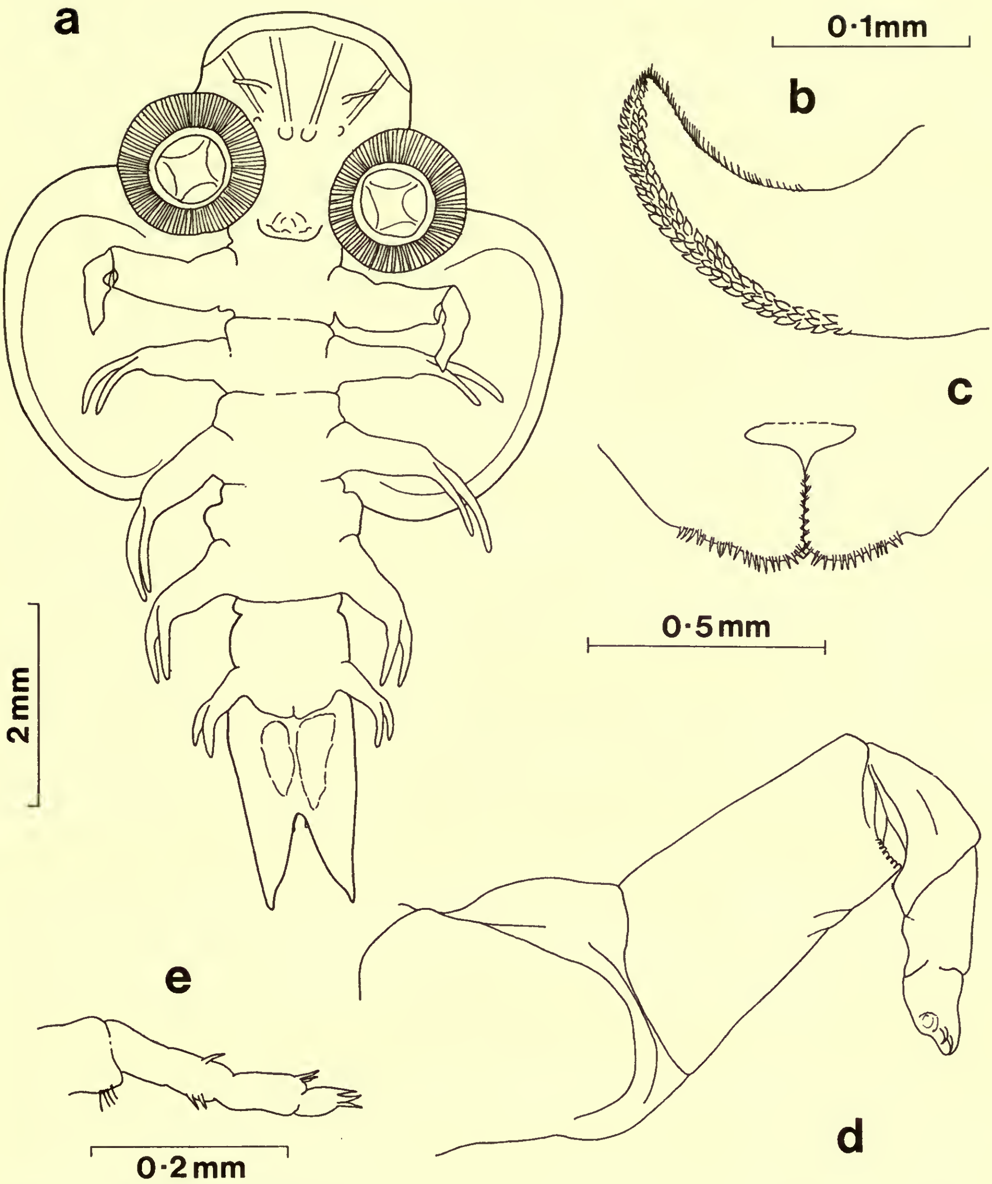
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FIG. 2. *Chonopeltis australis* sp. nov.: (a) adult female, ventral; (b) mandible, ventral; (c) natatory lobes female, ventral; (d) second maxilla female, ventral; (e) first antenna female, ventral.

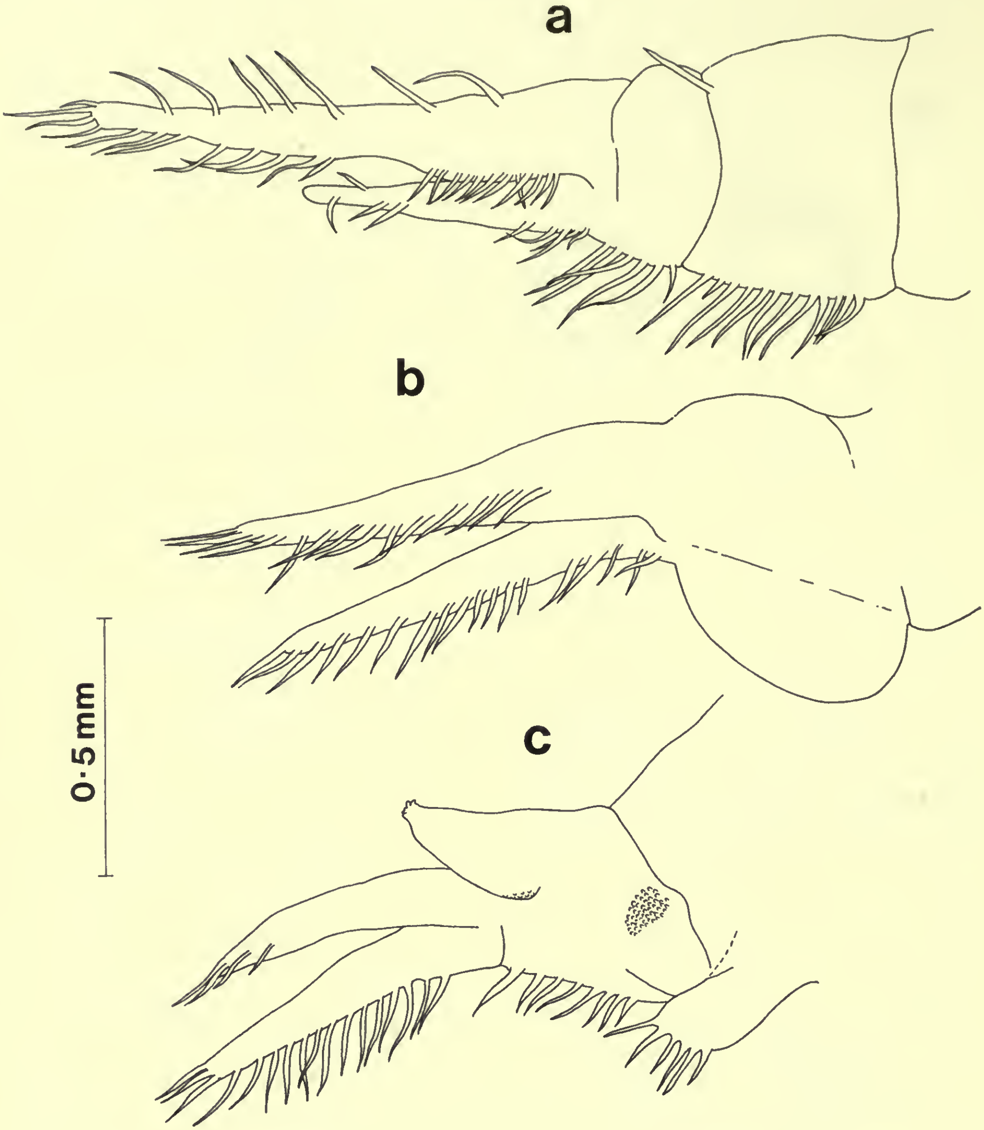

FIG. 3. *Chonopeltis australis* sp. nov. male: (a) leg 2; (b) leg 3; (c) leg 4.

Body length 5·0–8·9 mm, with a mean of 6·8 mm (based on 8 specimens).

Adult male. Carapace comprising about 57% and abdomen about 34% of total body length (Fig. 1b). Anterior appendages as in female. Legs 2–4 showing sexual characters; leg 2 without any projections on posterior margin of sympod (Fig. 3a); sympod of leg 3 (Fig. 3b) bearing an extensive marginal flap posteriorly; leg 4 (Fig. 3c) with an antero-laterally directed conical process on sympod, exopod simple without any processes.

Body length 3·8–5·8 mm, with a mean of 4·5 mm (based on 8 specimens).

MATERIAL EXAMINED. 9♀♀ (1 damaged) and 8♂♂ specimens. Holotype ♀ reg. no. 1975.1092 ; paratypes reg. nos 1975.1093–1108 ; deposited in the collections of the British Museum (Natural History).

DISTRIBUTION. *C. australis* was collected from the body surface of *Labeo capensis* Smith and *L. rosae* Steindachner caught at two sites : near Vereeniging on the Vaal river and near Potchefstroom, in the Boskop Dam reservoir on the Mooi river. Both the Vaal and the Mooi are part of the Orange river system.

REMARKS. The new species can readily be placed in a group of species, together with *Chonopeltis brevis* Fryer and *C. meridionalis*, which is characterized by the possession of two longitudinal bands of pigment spots on the thorax. Also in common with these species *C. australis* is found externally on the host. This is in keeping with the suggestion made by Fryer (1964) that the pigment bands serve to protect developing eggs in the uteri from intense illumination and are therefore found only in species of *Chonopeltis* which are external body surface parasites.

The males of *C. australis* can be distinguished from those of *C. brevis* and *C. meridionalis* by the absence both of any posterior projections on the sympod of leg 2 and of any process on the exopod of leg 4. The females of these three species are very similar and trivial morphological characters must be used to distinguish between them. In *C. brevis* leg 3 is more than twice as long as leg 4 whereas in *C. australis* and *C. meridionalis* it is less than twice as long. The natatory lobes of leg 4 in *C. meridionalis* are rounded and less extensive laterally than in *C. australis*. In addition the scale-covered prominence on the proximal portion of the second maxilla of *C. australis* is a distinctive character.

The structure of the second maxilla of *C. australis* suggests that it is able to function in a prehensile manner although it is not so obviously prehensile as in *C. schoudeteni* Brian and *C. flaccifrons* Fryer, both of which possess a large digitiform process on the proximal portion of the appendage.

ACKNOWLEDGEMENTS

I would like to thank Dr H. Schoonbee (Rand Afrikaans University, Johannesburg) for donating the material to the Museum and for providing data on the distribution of the species and Dr G. Fryer (Freshwater Biological Association) for reading and commenting upon the manuscript.

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MICROLAOPHONTE TRISETOSA SP. NOV., A NEW HARPACTICOID COPEPOD FROM SOUTHERN FLORIDA

By G. A. BOXSHALL

INTRODUCTION

THE copepod described below was isolated by Dr J. D. George (British Museum (Natural History)) from laboratory cultures of the polychaete *Capitellides giardi* Mesnil. Dr J. Fell and Mrs R. Hendrix (University of Miami) originally established the cultures by inoculating agar plates with decomposing mangrove leaves during investigations into the fungi and nematodes of the southern Florida red mangrove forest detrital system. The cultures have been successfully maintained since August 1972 and the culture technique, together with certain aspects of the biology of the new harpacticoid species, is described in detail by George (1976).

The material upon which this study is based was provided by Dr George in July 1975. It was examined both by phase contrast microscopy and by scanning electron microscopy (SEM). Drawings were made with the aid of a camera lucida and from SEM photographs.

DESCRIPTION OF NEW SPECIES

Microlaophonte trisetosa sp. nov.

TYPES. Holotype ♀ registration no. 1975.1255, allotype ♂ registration no. 1975.1256, paratypes registration nos 1975.1257–1267 ; deposited in the collections of the British Museum (Natural History). Cultures established using material collected near Matheson Hammock, Miami, Florida, U.S.A.

ADULT FEMALE. Body slender, cylindrical, with somites clearly defined (Fig. 1a–c). Cephalothorax about as long as 3 succeeding somites combined, with sensillae around its lateral and posterior margins. Rostrum short, with 2 sensillae. Each thoracic somite with a row of sensillae dorsally and laterally along the posterior margin. Genital double somite subdivided by a continuous dorsal and lateral chitinous strip armed with sensillae, posterior margin of double somite also provided with sensillae except on mid-ventral portion. Antepenultimate somite similarly provided with sensillae ; penultimate somite without sensillae but with a continuous ventro-lateral and ventral row of spinules. Anal somite with a sensilla on each side of the operculum and with a row of spinules ventrally and ventro-laterally around the bases of the caudal rami.

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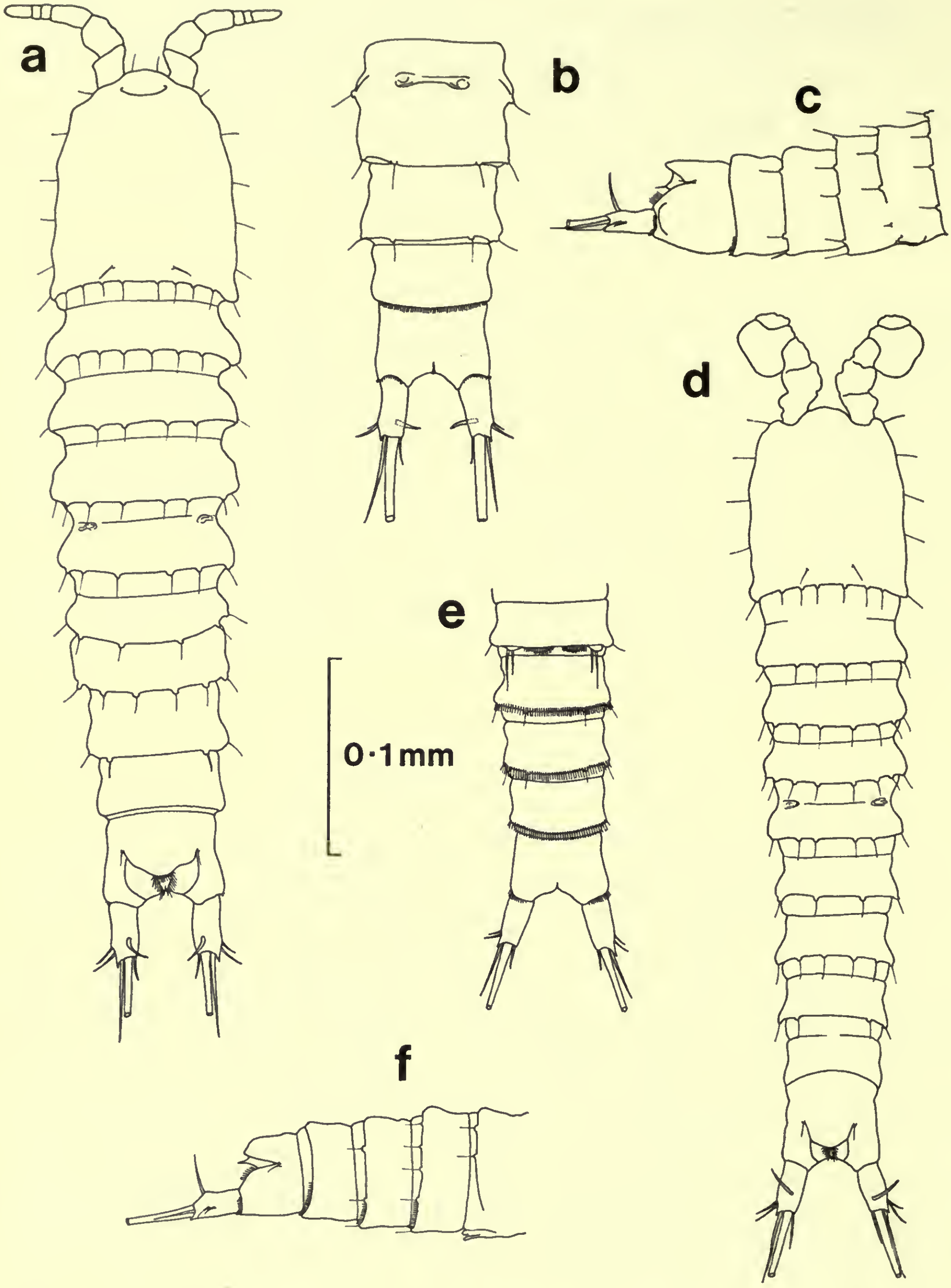

FIG. 1. *Microlaophonte trisetosa* sp. nov. : (a) female, dorsal ; (b) abdomen, ventral ; (c) abdomen, lateral ; (d) male, dorsal ; (e) abdomen, ventral ; (f) abdomen, lateral.

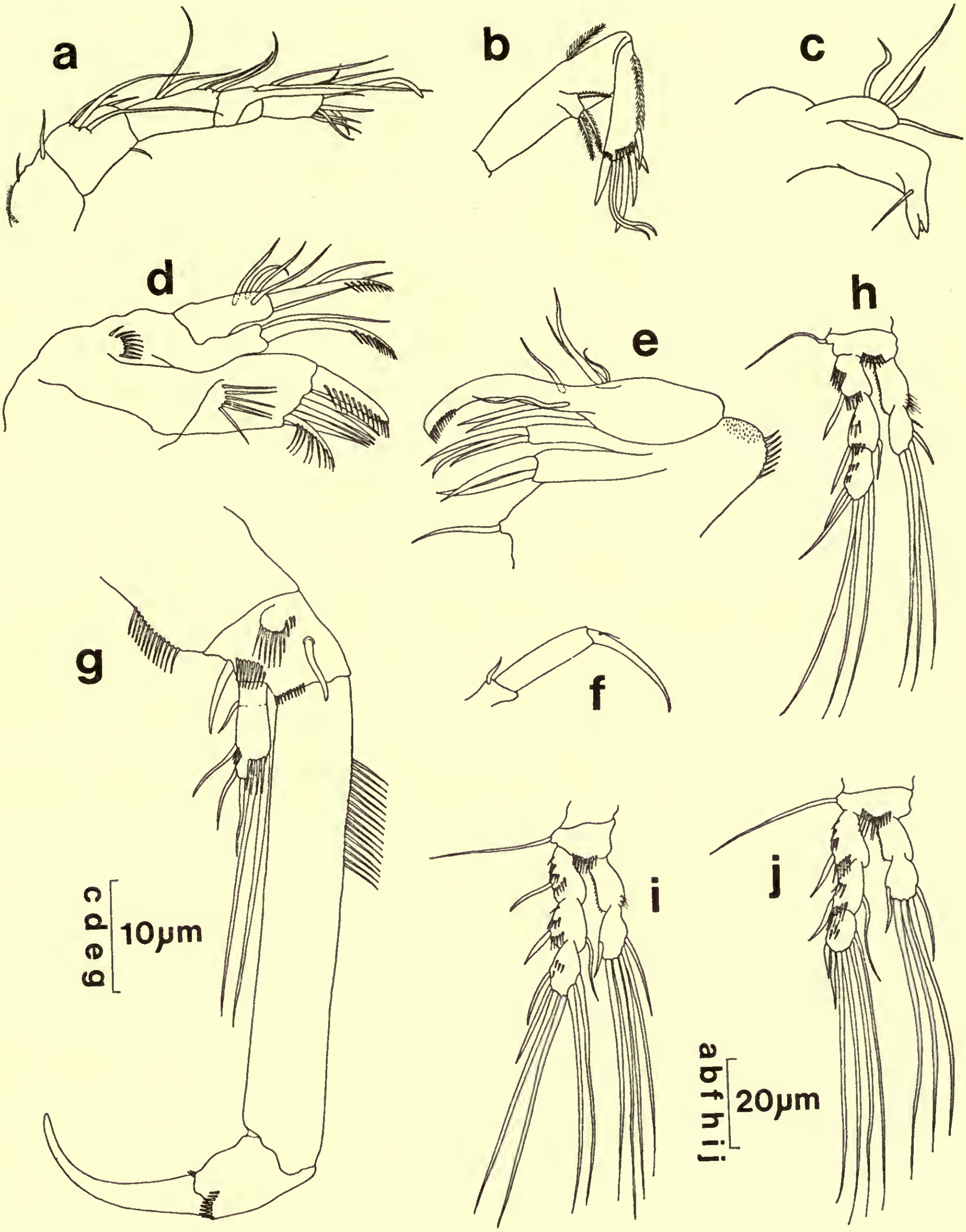
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FIG. 2. *Microlaophonte trisetosa* sp. nov. : (a) female first antenna, dorsal ; (b) second antenna, ventral ; (c) mandible, posterior ; (d) first maxilla, posterior ; (e) second maxilla, posterior ; (f) maxilliped, ventral ; (g) leg 1, anterior ; (h) leg 2, anterior ; (i) leg 3, anterior ; (j) leg 4, anterior.

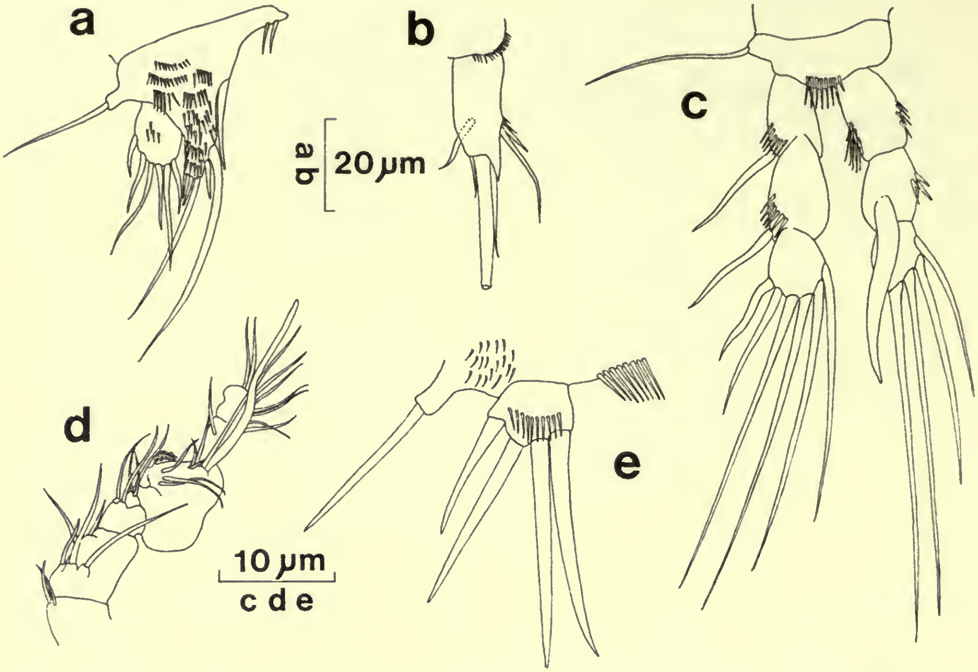

FIG. 3. *Microlaophonte trisetosa* sp. nov. : (a) female leg 5, anterior ; (b) caudal ramus, ventral ; (c) male leg 3, anterior ; (d) first antenna, dorsal ; (e) leg 5, ventral.

Caudal rami (Fig. 3b) not markedly divergent, about 2 times longer than broad ; with a pointed process at the postero-lateral angle ; whole surface with densely scattered minute spinules.

First antenna (Fig. 2a) 6-segmented, third segment longest, about 3 times longer than fourth which carries a long aesthetasc ; last segment longer than 2 preceding segments combined.

Second antenna (Fig. 2b). Coxa unarmed ; allobasis with a plumose seta on outer margin ; exopod small bearing 1 lateral and 2 apical plumose setae. Endopod becoming flattened distally, with a dense covering of spinules and 1 distal spine on anterior margin, 4 strong spines and 2 geniculate setae on the distal margin and 2 spinule rows near apex on ventral surface.

Mandible (Fig. 2c). Praecoxa provided with a bidentate pars incisiva and a strong spine terminally and a slender seta subterminally. Palp 1-segmented with 1 apical and 3 lateral setae.

First maxilla (Fig. 2d). Arthrite of praecoxa with a proximal row of slender spinules and, along the distal margin, 1 very robust spine with spinules, about 5 slender spines and a spinulate seta. Coxa with a proximal row of spinules and 2 terminal setae, 1 spinulate distally ; basis with 3 apical setae, 1 strong and distally spinulate ; endopod represented by 4 setae.

Second maxilla (Fig. 2e). Syncoxa with 3 endites : proximal endite short with a single seta ; middle endite with 2 stout setae ; distal endite with 3 setae. A row of spinules and a patch of minute denticles also present at outer corner of syncoxa. Basis drawn out into a slightly curved claw accompanied by 1 anterior, 1 posterior and 2 dorsal setae ; endopod represented by 3 setae.

Maxilliped (Fig. 2f). Basis with a single seta ; endopod 2-segmented with apical segment forming a slender claw bearing a spinule basally.

Leg 1 (Fig. 2g). Coxa with spinule row along outer margin ; basis with proximal spinule row around a small anterior tubercle, a spinule row near base of endopod, another row near base of exopod and 2 setae, 1 located on outer margin proximal to the exopod and the other on the anterior surface near the inner margin. Exopod 1-segmented, although in some specimens an incipient subdivision is apparent, with 1 proximal and 2 distal setae on the outer margin, 1 short and 2 long setae on the distal margin and a distal spinule row. Endopod well developed ; first segment long with spinules on proximal portion of inner margin, second segment with spinules on inner and outer edges ; third segment forming a curved claw.

Legs 2–4 (Fig. 2h–j). Coxa unarmed ; basis with an outer seta and a single spinule row on ventral surface between bases of rami. Exopod 3-segmented ; first and second segments similar in length and longer than third ; rows of spinules present on all exopod segments. Endopod 2-segmented ; first segment larger, with minute spinules on lateral surface and longer hairs on inner surface ; second segment of leg 2 with a conspicuous proximal spinule ; endopod of leg 4 shorter, not reaching beyond end of second exopod segment. Spine and seta formula :

	Exopod			Endopod	
	1	2	3	1	2
Leg 2	0	1	2 1 2	0	2 2 0
Leg 3	0	1	2 2 2	0	3 2 1
Leg 4	0	1	2 2 2	0	2 2 1

Spines and setae closely approximated and exact point of insertion on internal or distal margin sometimes difficult to discern.

Leg 5 (Fig. 3a). Baseoendopod longer than exopod ; anterior surface with many rows of spinules ; outer margin with a single seta, inner margin with 2 proximal spinules, 1 seta at the base of the endopod portion and a spine and a long seta distally ; distal margin with 1 seta and 2 spines. Exopod with 4 spinules on anterior surface and with 6 setae around the outer and distal margins.

Ovisac with 6–10 eggs.

Body length of female ranging from 0·47 to 0·51 mm, with a mean of 0·49 mm.

ADULT MALE. Body more slender and shorter than female (Fig. 1d–f). Ornamentation of abdominal somites similar to female but with additional ventral spinule rows located anterior to the sensillae on the ante- and penultimate somites.

First antenna (Fig. 3d) 6-segmented, subchirocerate ; aesthetasc present on fourth segment.

Legs 2 and 4 as in female but outer spines on exopod longer and more robust ; inner seta on second exopod segment usually absent from leg 4. Leg 3 (Fig. 3c) with 3-segmented endopod ; second segment with a mucroniform process at outer distal corner, third segment with 4 setae.

Leg 5 (Fig. 3e). Baseoendopod with a spinule row on inner margin, a long seta on outer margin and some scattered spinules located anterior and lateral to base of exopod; exopod broader than long, with a row of spinules, 1 seta at outer distal corner and 3 distal setae.

Leg 6. Each leg comprising a long outer seta and a short inner seta.

Mean body length 0·40 mm, with a range of 0·38 to 0·43 mm.

Variation. Ten specimens of each sex were dissected to examine possible variation in the armature of legs 2–4. No variation was found in the female. In the male the inner seta of exopod segment 2 was present on leg 2 in all 10 specimens, on leg 3 in 5 specimens and on leg 4 in only 2 specimens. No other variability was observed.

REMARKS

The new species is provisionally assigned to the genus *Microlaophonte* Vervoort, 1964 in the subfamily Laophontinae. There are marked differences between the new species and *M. spongicola* Vervoort, 1964, the type and only species of the genus, but these are not sufficient to justify the establishment of a new genus. However, *M. spongicola* is known only from the female (Vervoort, 1964) and the eventual discovery of the male may necessitate the removal of *M. trisetosa* from the genus if the male secondary sexual characters are found to differ significantly from those of *M. trisetosa.*

The spine and seta formula of legs 2–4 is of diagnostic importance at the generic level in the Laophontidae. The formulae of *M. spongicola* and *M. trisetosa* differ primarily in the presence of an additional internal seta on the second endopod segment of legs 2 and 3 in the latter species. However, the absence of the small innermost seta on this segment in *M. spongicola* may only be apparent as Vervoort (1964) states that small setae may have been obscured by the hairs on the endopod.

The two species can be readily separated by the presence in *M. trisetosa* of 3 setae on the exopod of the second antenna (the character alluded to in the specific name), of 6 setae on the exopod of leg 5 in the female and by the 1-segmented nature of the exopod of leg 1.

ACKNOWLEDGEMENTS

I am indebted to Dr George for providing the material for this study and to Dr R. J. Lincoln for his critical reading of the manuscript.

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A NEW SPECIES OF *AMPHITHOE (PLEONEXES)* (AMPHIPODA: AMPHITHOIDAE) FROM THE NORTH-EAST ATLANTIC WITH A REDESCRIPTION OF *A. (P.) GAMMAROIDES* (BATE)

By ROGER J. LINCOLN

INTRODUCTION

A SHORT review of the subgenus *Pleonexes* is given in a recent paper by Mateus & Afonso (1974) together with a table of comparative characters for the six recognized species. *Pleonexes* was only recently relegated from the familiar generic status to that of a subgenus by Barnard (1970) on the evidence of a gradation of characters between *Amphithoe* and *Pleonexes*. The subgenus is identified in the Atlantic by the marked expansion of the propodus of pereopods 5–7 and the pair of prominent hooked spines on the distal margin of the telson, although an examination of all *Amphithoe* species reveals a gradation of these characters which suggests that *Pleonexes* may not be a valid subgenus.

Only three species of *Amphithoe* (*Pleonexes*) are recognized from the north-east Atlantic and Mediterranean, namely *A.* (*P.*) *bicuspis* (Heller) from the Adriatic, *A.* (*P.*) *pomboi* Mateus & Afonso from the Azores and *A.* (*P.*) *gammaroides* (Bate), which is the only widespread species recorded along the coast of Europe from southern Norway to the western Mediterranean and including the British Isles.

After examining the amphipods in the British Museum (Natural History) as part of the preparation for a new handbook on the amphipod fauna of the British Isles, it is clear that there are in fact two quite distinct species of *Pleonexes* in collections from British localities. The two species differ considerably in body size and especially in the relative proportions and robust nature of the antennae, as well as other structural characters. Collections from more northerly areas, especially Shetland Isles and the west coast of Scotland, consist only of the larger of the two species which is the true *gammaroides*, while material from the south coast of England, southern and south-western Ireland belongs mostly to the new and smaller species which is described below as *Amphithoe* (*Pleonexes*) *neglectus* n. sp.

The confusion over the identification of the two species can probably be explained by the fact that Sars (1894), in his excellent monograph on the amphipods of Norway, figured the female of the true *gammaroides* (actually a specimen from southern Norway originally ascribed to *Sunamphithoe hamulus* by Boeck but now recognized to be a synonym of *gammaroides*), while his figures of the male are not of *gammaroides* but the new species, *neglectus*. Fortunately, Sars offers an explanation of this in his

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text (page 584) where he states that he had no male specimen of *gammaroides* from Norway and had illustrated material collected in France.

Two other species should be referred to the synonymy of *gammaroides*, namely *Sunamphithoe longicornis* Boeck and *Sunamphithoe hamulus* Bate. An examination of the type *S. hamulus* has shown it to be the female of *gammaroides* and not of *Sunamphithoe conformata* Bate as proposed by Stebbing (1906).

DESCRIPTION OF SPECIES

Amphithoe (Pleonexes) neglectus n. sp.

(Figs 1a ; 2a–h ; 3a–g ; 4a–g)

Pleonexes gammaroides : Sars, 1894 : 582 (part), pl. 207 (♂) ; Stebbing, 1906 : 642 (part).

Diagnosis. Length up to 5 mm ; antennae subequal, moderately setose, equal to half body length or less. Gnathopod 1 propodus elongate oval. Gnathopod 2 ischium without distinct lobe on anterior margin ; in male propodus broadly oval, tumid, palmar surface concave with distinct inner and outer palmar margin, delimited from posterior margin by rounded angle. Pereopod 5 basis very much expanded, broader than long. Telson with prominent marginal hooks and pair of mediolateral setae.

Description. Length 4–5 mm, body rather slender, compressed, urosome segment 1 with pair of dorsal setules (Fig. 1a) ; colour in spirit whitish with scattered dark chromatophores on body, coxal plates, basal segments of pereopods and antennal peduncles. *Coxal plates* 1–5 moderately large, distal margins rounded with numerous small setules ; coxal plate 1 produced slightly forwards ; plate 2 with anterior margin very broadly rounded ; plate 4 entire, not excavate posteriorly ; plate 5 with small posterior lobe, and large anterior lobe about equal to length of plate 4. *Epimeral plates* 1–3 rounded ; plates 2–3 (Fig. 4c) with small setule inset in posterodistal margin. *Head* with lateral lobes broadly convex, only moderately produced ; eyes small and rounded, visual elements distinct. *Antennae* (Fig. 2a, b) relatively short and setose, equal or little less than half body length, of subequal length or with antenna 1 little longer than 2 ; accessory flagellum absent ; antenna 1 peduncle article 1 robust with 2–3 distoventral, and 1–2 small mid-ventral, spinules ; article 2 little shorter than 1 ; article 3 about half length of 2 ; flagellum about 15 to 18-articulate, each article with distinct elongate aesthetasc ; antenna 2 more robust than 1 especially in male, peduncle articles 4 and 5 subequal, or article 5 slightly longer than 4 ; flagellum moderately setose, shorter or equal to peduncle article 5, about 9-articulate with proximal articles often swollen (Fig. 2b). *Upper lip* entire, margin rounded, setulose. *Mandible* with distinct molar ; left mandible (Fig. 2f) with 5 spines in spine-row, right mandible (Fig. 2g) with 4 spines ; palp 3-articulate, article 1 short, article 2 with single large distal seta, article 3 with group of about 9 large terminal setae. *Lower lip* (Fig. 2c) with inner and outer lobes distinct, setulose. *Maxilla* 1 (Fig. 2d) inner plate very small with single small seta, outer plate with about 9 robust spines ; palp 2-articulate, article 1 very short, article 2 elongate and curved, reaching beyond apex of outer plate with 2–3 small

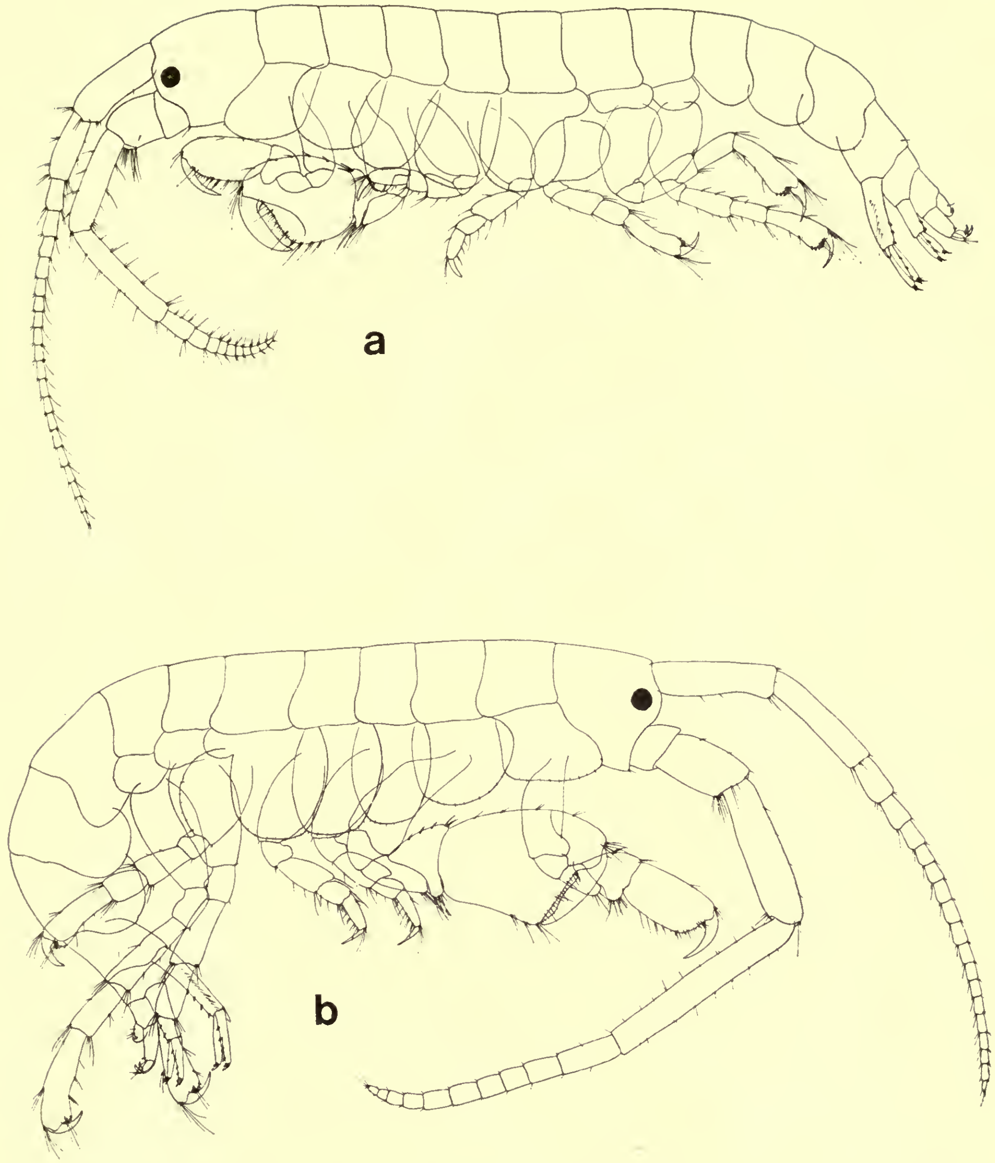

FIG. 1. (a) *Amphithoe* (*Pleonexes*) *neglectus* n. sp. male, entire ; (b) *Amphithoe* (*Pleonexes*) *gammaroides* (Bate), male, entire.

terminal spines. *Maxilla* 2 (Fig. 2e) inner plate with several long, inner-marginal, plumose setae ; inner margin also fringed with fine short setules ; outer plate longer than inner, outer and distal margins fringed with fine short setules, distal margin with several long setae. *Maxilliped* (Fig. 2h) inner plate short ; outer plate elongate oval with inner margin finely serrate, marginal spines increasing in length distally ; palp 4-articulate, setose. *Gnathopod* 1 (Figs 3a, 4f) generally similar in male and female ;

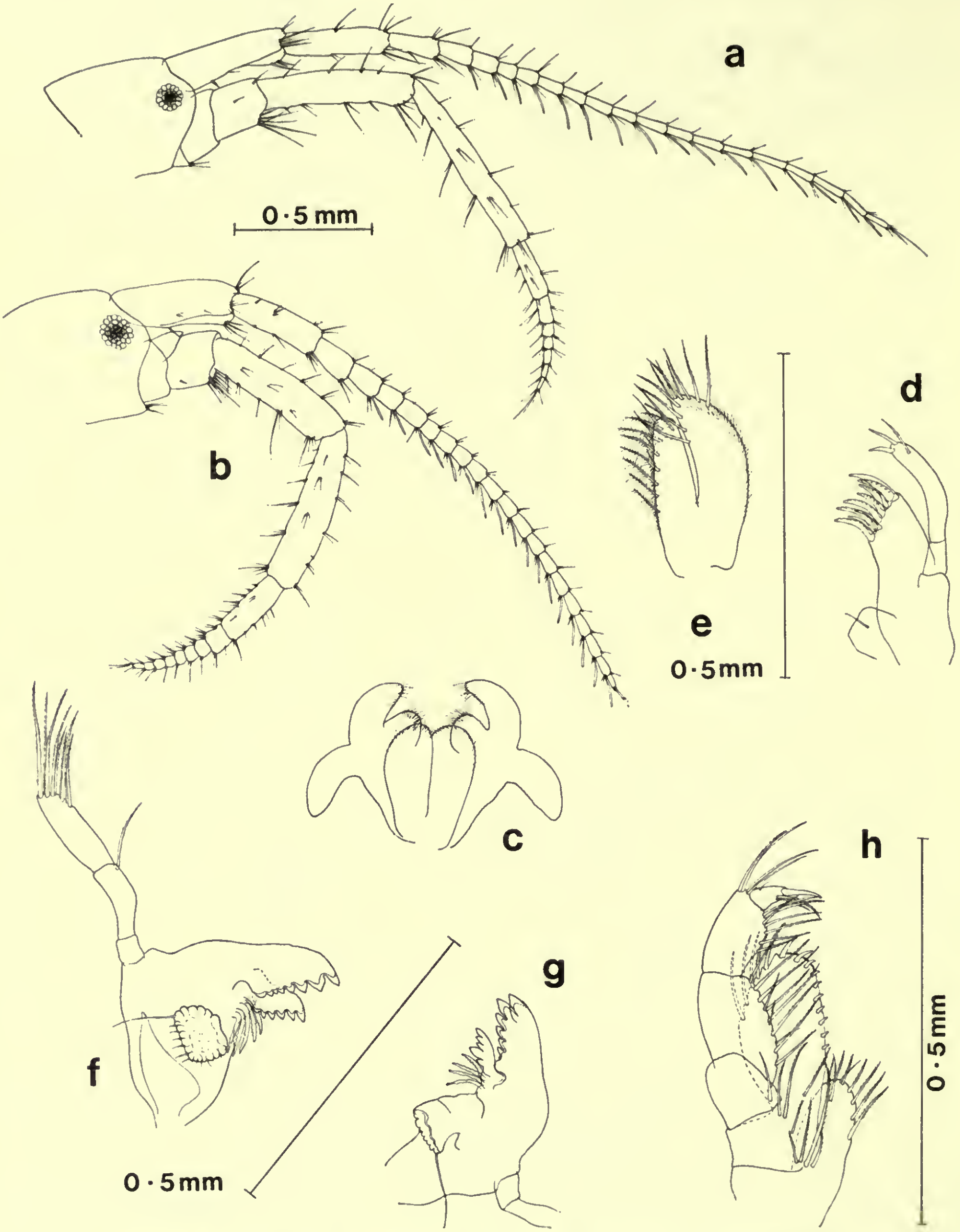
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Fig. 2. *Amphithœ* (*Pleonexes*) *neglectus* n. sp. male ; (a) head and antennae ; (b) head and antennae, robust ; (c) lower lip ; (d) maxilla 1 ; (e) maxilla 2 ; (f) left mandible ; (g) right mandible ; (h) maxilliped.

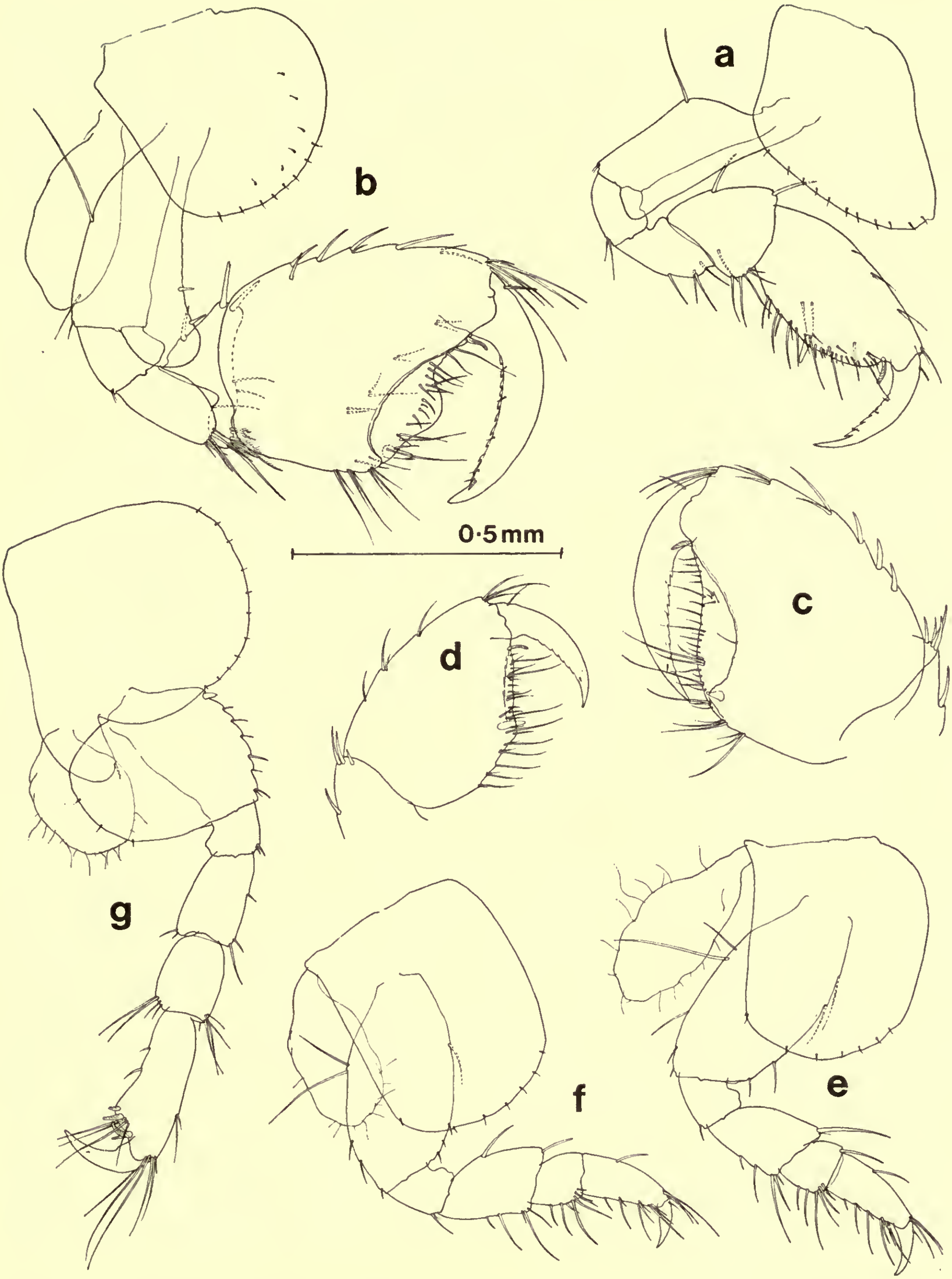

FIG. 3. *Amphithoe* (*Pleonexes*) *neglectus* n. sp. male ; (a) gnathopod 1 ; (b) gnathopod 2 ; (c) gnathopod 2, propodus ; (d) gnathopod 2, propodus, small male ; (e) pereopod 3 ; (f) pereopod 4 ; (g) pereopod 5.

basis robust, narrow proximally with posterior margin rather angular, anterodistal angle with small rounded lobe ; merus with few distal setae ; carpus much shorter than propodus, anterior margin convex with large median spine and 1–2 large distal spines, posterior margin rounded with few long setae ; propodus elongate oval, palm convex and poorly defined from posterior margin, delimited by single large spine, distal margin of palm with single curved striated spine close to base of dactylus, posterior and palmar margins moderately setose ; dactylus little longer than palm, inner margin toothed. *Gnathopod 2 female* (Fig. 4g) little larger and more robust than 1 ; basis with large anterodistal lobe bearing 1–2 small spinules ; carpus with posterior lobe rather slender and produced ; propodus broadly oval, anterior margin with 4–5 small groups of setae, palm convex, oblique, delimited from posterior margin by obtuse angle and single large spine ; posterior and palmar margins strongly setose, palmar margin with single curved, striated, spine close to base of dactylus. *Gnathopod 2 male* (Fig. 3b) very much larger and more robust than in female ; basis with very large anterodistal lobe bearing 2–3 small spines ; carpus very short with slender posterior lobe, anterior margin with strong median and distal spines ; propodus very broad and robust, anterior margin strongly convex with several small groups of setae or spines, palm complex with concave surface between distinct inner and outer palmar margins (Fig. 3c), delimited by obtuse angle and single stout spine ; in smaller specimens the outer palmar margin may be indistinct (Fig. 3d) ; palm weakly setose with single striated spine close to base of dactylus. *Pereopods* 3–4 (Fig. 3e, f) basis narrowly oval, anterior and posterior margins weakly setose ; merus broad distally ; carpus short ; propodus about equal to length of merus, tapering distally ; dactylus weakly curved and about half length of propodus ; merus, carpus and propodus with few long setae. *Pereopod* 5 (Fig. 3g) basis broader than long with very large posterior lobe, anterior margin with several short spines ; merus little longer than carpus ; propodus broad distally, palm with 3–4 short, and 1 long curved, striated spines ; inner and outer palmar surface with small group of long setae. *Pereopod* 6 (Fig. 4a) more elongate than 5 ; basis with moderately large posterior lobe which narrows distally to produce sinuous posterior margin ; merus, carpus and propodus similar to pereopod 5 only more elongate. *Pereopod* 7 (Fig. 4b) slightly longer than 6 ; basis narrowly oval with only small posterior lobe and convex posterior margin. *Uropods* (Fig. 4d) short and spinose. *Uropod* 1 peduncle with 3 distomarginal spines and many long outer-marginal setae, distoventral angle with short blunt process ; outer ramus with about 3 marginal spines and small group of terminal spines ; inner ramus equal to length of outer, with only small group of apical spines. *Uropod* 2 peduncle with 2 distomarginal spines ; outer ramus with 2 marginal spines ; inner ramus equal to length of outer, with only apical spines. *Uropod* 3 (Fig. 4e) peduncle robust with single distal spine ; outer ramus with pair of large curved spines and finely denticulate dorsal margin ; inner ramus with small apical spine and about 6 long setae. *Telson* fleshy, entire, with distinct distolateral hooks and pair of mediolateral setae.

HOLOTYPE. Portsmouth, ♂ collected from *Sargassum*. BM(NH) reg. no. 1975:467:1.

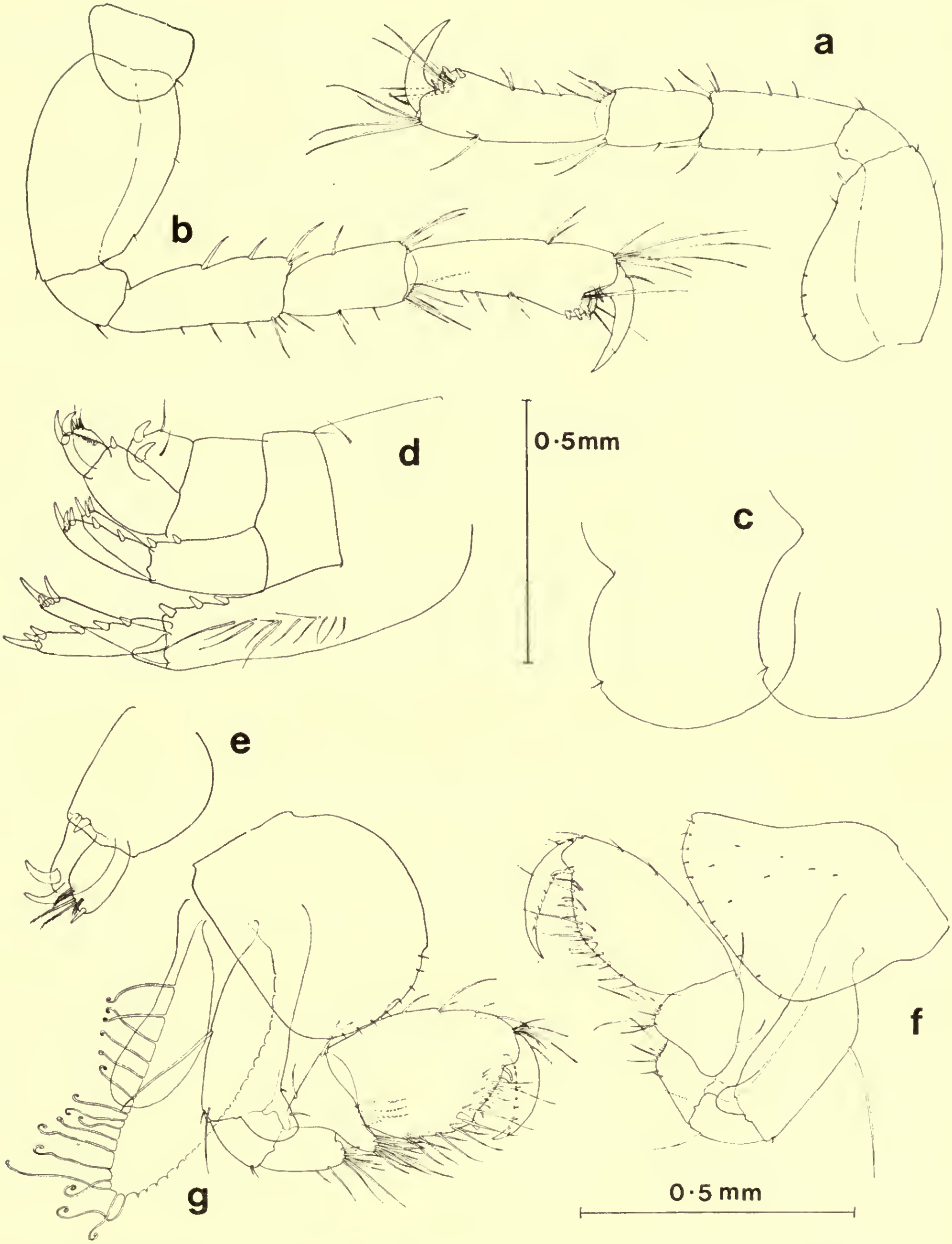

FIG. 4. *Amphithoe* (*Pleonexes*) *neglectus* n. sp. a–e, male ; f–g, female : (a) pereopod 6 ; (b) pereopod 7 ; (c) epimeral plates 2–3 ; (d) urosome and uropods ; (e) uropod 3, inner aspect ; (f) gnathopod 1, female ; (g) gnathopod 2, female.

OTHER MATERIAL EXAMINED

Portsmouth: 7♂♂, 3♀♀ collected from *Sargassum*. BM(NH) reg. no. 1974:365:10.

Loch Ine, Ireland: 5♂♂, 30♀♀, 20 juv. collected from *Codium* and *Stilophora*, all specimens damaged. BM(NH) reg. no. 1975:464:55.

Loch Ine, Ireland: 5♂♂, 18♀♀, 10 juv. collected from *Codium* and *Stilophora*. BM(NH) reg. no. 1975:465:33.

Trevone Bay, Cornwall: 3♀♀ from algae at low-water. BM(NH) reg. no. 1974:366:3.

Portnafranca, Co. Mayo, Ireland: 1♀ BM (NH) reg. no. 1971:63:1.

Colieragh Bay, Bantry Bay, Ireland: 1♂, 3♀♀ collected from low water. BM(NH) reg. no. 1975:466:4.

REMARKS. The propodus of the second gnathopod shows a considerable range of development in the male. In small specimens the palm is almost straight with only little evidence of the concave surface and outer palmar margin (Fig. 3d). However, in large males the propodus is very robust and swollen with a broadly concave palmar surface and distinct inner and outer margin. A small amount of variation is also evident in the second antenna which may be slender in females and some males, while in others the peduncle is quite robust and the basal articles of the flagellum are distinctly swollen (Fig. 2b).

The new species, *neglectus*, is most closely allied to the Mediterranean *bicuspis* figured by Giordani Soika (1950) which also has the broad palm on the male second gnathopod. However, the two species can be separated by the detailed structure of the male and female gnathopods, the setation of the pereopods and the arrangement of spines on the propodal articles, as well as other differences in relative proportions and setation.

Amphithoe (Pleonexes) gammaroides (Bate)

(Figs 1b; 5a–g; 6a–e; 7a–g)

Pleonexes gammaroides Bate, 1857: 147; Stebbing, 1906: 642 (part); Sars, 1894: 582 (part) pl. 207 (♀); Chevreux & Fage, 1925: 335, fig. 344.

Amphithoe gammaroides: Bate, 1862: 235, pl. 41, fig. 4; Bate & Westwood, 1863: 427.

Sunamphithoe hamulus Bate, 1857: 148; 1862: 250, pl. 43, fig. 5; Bate & Westwood, 1863: 430; Boeck, 1872: 594, pl. 27, fig. 1.

Sunamphithoe longicornis Boeck, 1870: 165; 1872: 596, pl. 27, fig. 2.

DIAGNOSIS. Length up to about 8 mm; antenna 2 longer than 1, sparsely setose especially in male, robust and much more than half body length. Gnathopod 1 propodus rather rectangular, palm oblique. Gnathopod 2 ischium with large asymmetrical lobe on anterior margin; in male propodus very broad, palm straight and finely toothed, delimited by distinct angle from posterior margin, distal part of anterior margin expanded towards base of dactylus. Pereopod 5 basis only moderately expanded, longer than broad. Telson with pronounced marginal hooks and numerous dorsal setules.

DESCRIPTION. Length 6–8 mm; urosome segment 1 with pair of dorsal setae; colour bright green with scattered dark chromatophores on sides of body. *Coxal plates* moderately large, margins rounded with numerous short setules; coxal plate 1

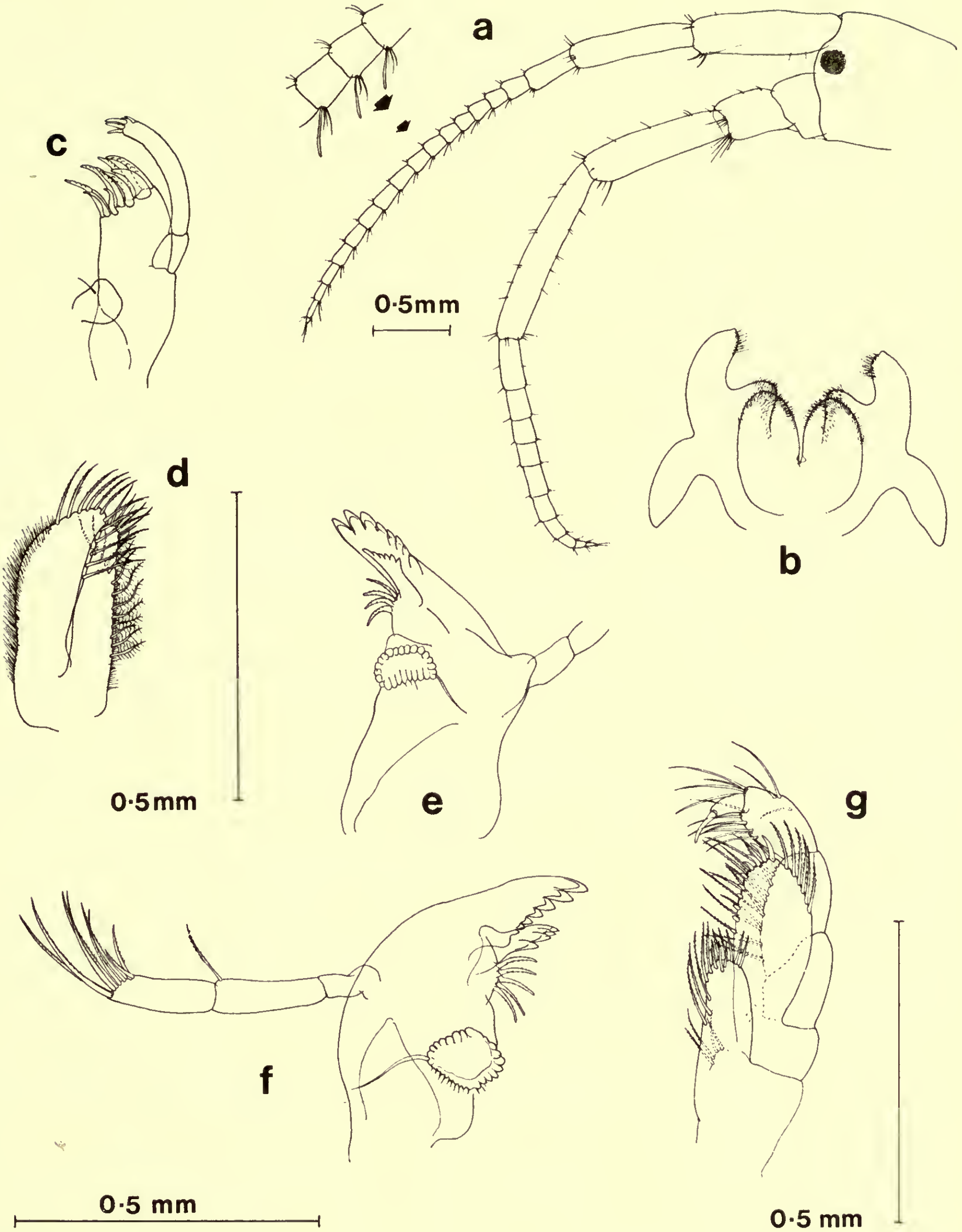
a
c
0·5mm
b
d
0·5mm
e
g
f
0·5 mm
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FIG. 5. *Amphithoe* (*Pleonexes*) *gammaroides* (Bate), male: (a) head and antennae, large male; (b) lower lip; (c) maxilla 1; (d) maxilla 2; (e) right mandible; (f) left mandible; (g) maxilliped.

produced slightly forwards ; plate 2 very broadly rounded ; plate 5 with anterior lobe equal to length of plate 4. *Epimeral plates* 1–3 (Fig. 7c) rounded. Head with lateral lobes convex, weakly produced ; eyes small and rounded, visual elements distinct. *Antennae* relatively long and robust, sparsely setose (Fig. 5a) ; antenna 1 equal to, or often little more than, half body length, peduncle article 1 robust with 3–4 distoventral and 1–2 mid-ventral spinules, article 2 equal to length of 1 ; flagellum up to about 18-articulate, each article with slender aesthetasc, setae very sparse and small ; antenna 2 more robust and much longer than 1, up to about two-thirds body length, peduncle article 5 longer than 4, flagellum about 9 to 13-articulate, also with only few small setae, flagellar articles often very robust in large specimens. *Upper lip* entire, setulose. *Mandible* with well developed molar, palp 3-articulate, article 2 with single long distal seta, article 3 with group of long apical setae ; left mandible (Fig. 5f) with 5 spines in spine row, right mandible (Fig. 5e) with 4 spines. *Lower lip* (Fig. 5b) with inner and outer lobes distinct, setulose. *Maxilla* 1 (Fig. 5c) inner plate small with single seta ; outer plate with about 9 robust spines ; palp 2-articulate, article 2 elongate, curved, with 3–4 small apical spines. *Maxilla* 2 (Fig. 5d) inner plate with several long plumose setae, inner margin fringed with fine setules ; outer plate longer than inner, outer and distal margins fringed with fine short setules, distal margin with several long setae. *Maxilliped* (Fig. 5g) inner plate short, setose ; outer plate elongate, oval, with inner margin finely serrate, marginal spines increasing in length distally ; palp 4-articulate, setose. *Gnathopod* 1 (Figs 6a, 7f) generally similar in male and female ; basis robust, narrow proximally, anterodistal angle with rounded lobe bearing 1–2 small spinules ; carpus much shorter than propodus, anterior margin with median spine and 1–2 large distal spines, posterior margin rounded, setose ; propodus elongate, palm convex and delimited by single large spine, posterior margin about straight, setose ; palmar margin setose with single curved striated spine close to base of dactylus. *Gnathopod 2 female* larger and more robust than 1 (Fig. 7g) ; basis with very large anterodistal lobe bearing 2–3 small spinules ; ischium with large asymmetrical lobe on anterior margin ; carpus with posterior lobe rather slender and produced ; propodus broadly oval, palm convex, oblique, delimited by obtuse angle and single large spine ; posterior and palmar margins strongly setose, palm with single striated spine close to base of dactylus. *Gnathopod 2 male* (Fig. 6b) very much larger and more robust than in female ; basis with large anterodistal lobe ; ischium with large asymmetrical lobe on anterior margin ; carpus very short, anterior margin with about 5 strong spines, posterior lobe slender and elongate ; propodus very broad, posterior margin about straight, palm long, oblique, straight with margin finely toothed, palm delimited by distinct angle and single stout spine ; anterior margin of propodus expanded distally to produce a rounded lobe at base of dactylus. *Pereopods* 3–4 (Fig. 6c, d) basis narrowly oval ; merus broad distally with anterior angle somewhat produced ; carpus short ; propodus about equal to length of merus, tapering distally ; dactylus only weakly curved and about half length of propodus. *Pereopod* 5 (Fig. 6e) basis broadly expanded but still longer than wide ; merus longer than carpus ; propodus broad distally, palm with 3–4 short spines and 1 long curved spine, inner and outer palmar surface with small group of long setae. *Pereopod* 6 (Fig. 7a) longer than 5 ;

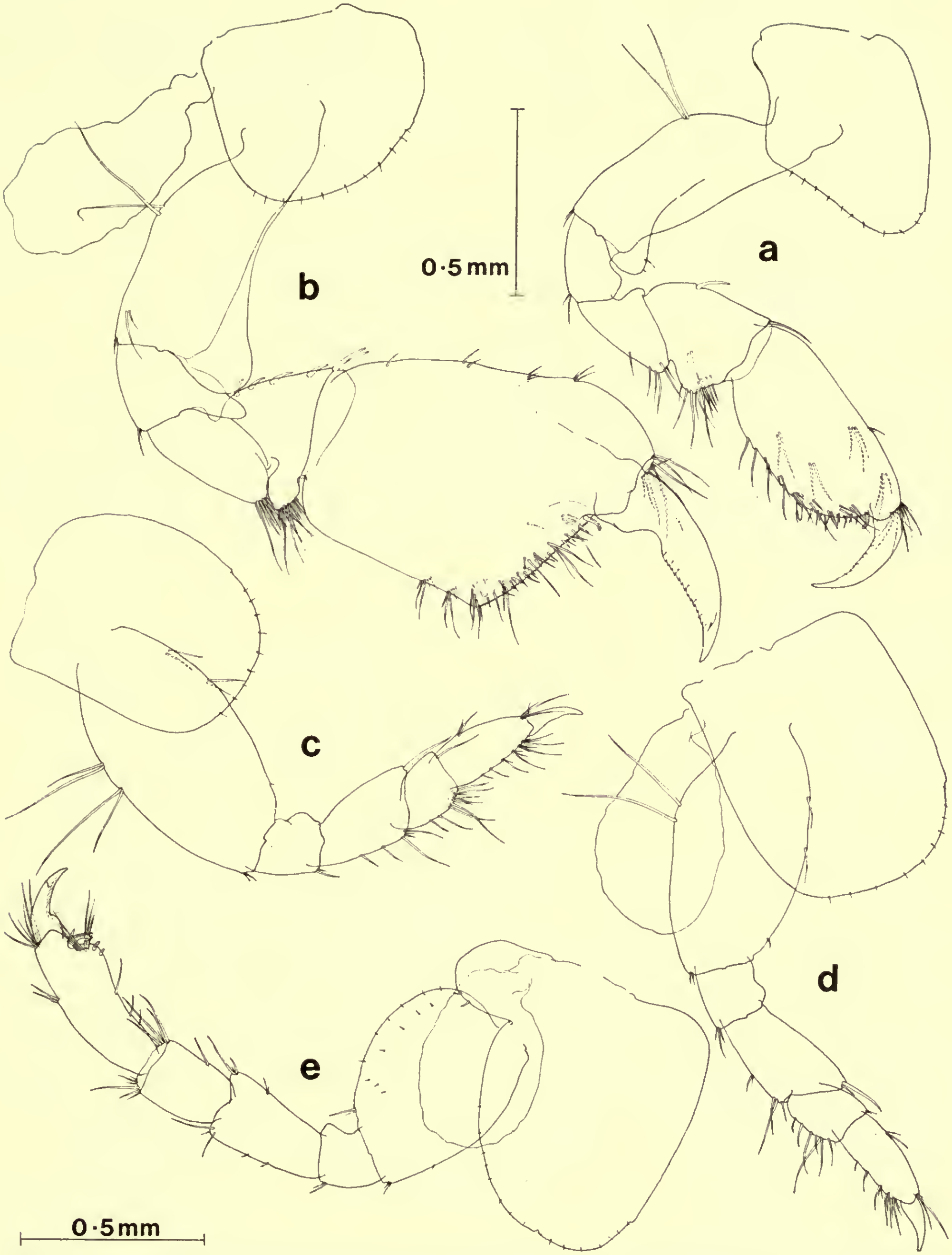

FIG. 6. *Amphithoe* (*Pleonexes*) *gammaroides* (Bate), male : (a) gnathopod 1 ; (b) gnathopod 2 ; (c) pereopod 3 ; (d) pereopod 4 ; (e) pereopod 5.

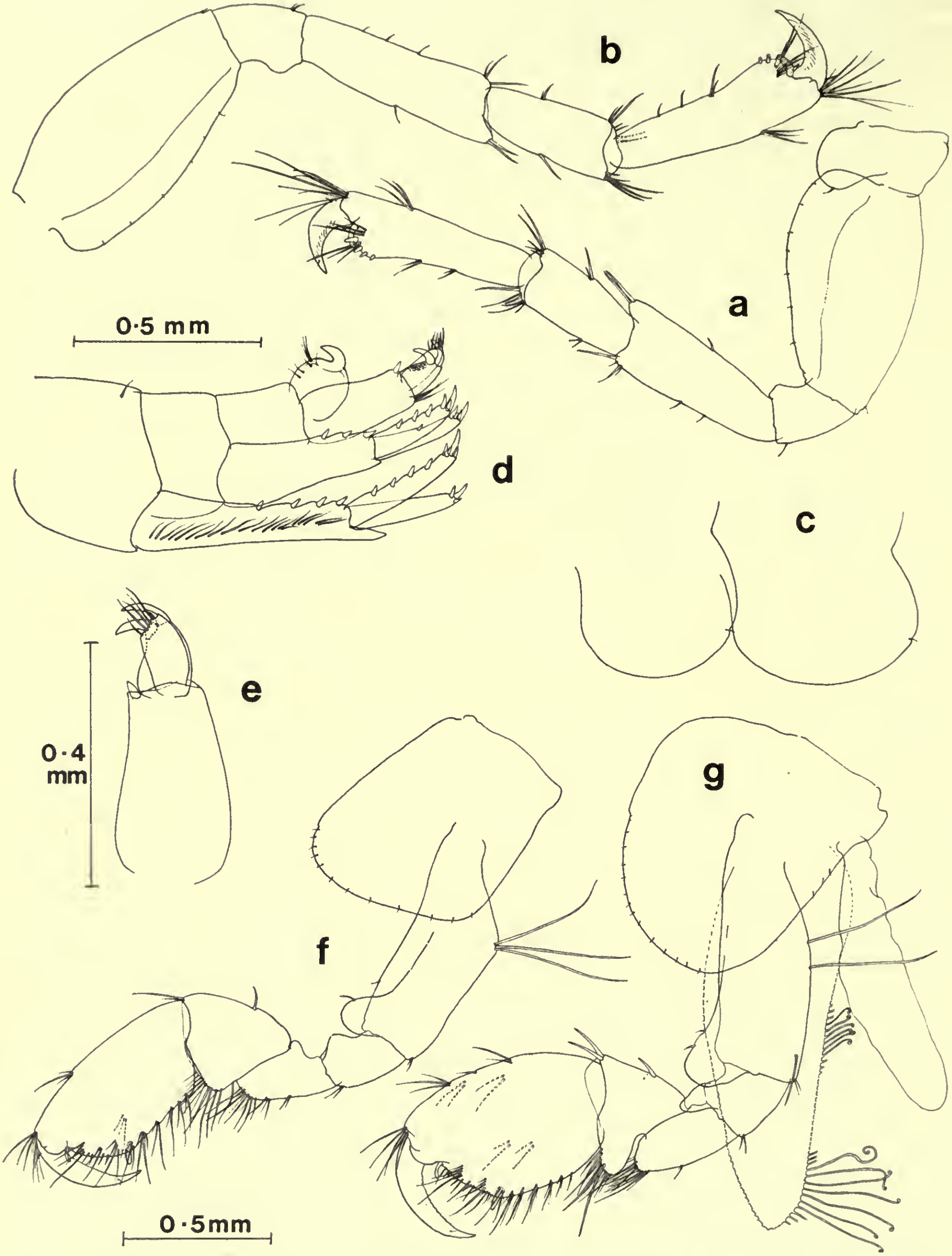

FIG. 7. *Amphithoe* (*Pleonexes*) *gammaroides* (Bate), a–e, male ; f–g, female : (a) pereopod 6 ; (b) pereopod 7 ; (c) epimeral plates 2–3 ; (d) urosome and uropods ; (e) uropod 3, inner aspect ; (f) gnathopod 1, female ; (g) gnathopod 2, female.

basis with moderately large posterior lobe which narrows distally ; merus, carpus and propodus similar to pereopod 5 only more elongate. *Pereopod* 7 (Fig. 7b) little longer than 6 but generally similar ; basis only narrowly oval with weakly convex posterior margin. Uropods (Fig. 7d) moderately elongate and spinose. *Uropod* 1 peduncle with 4 distomarginal spines and numerous long outer-marginal setae, distoventral angle with large blunt process ; outer ramus with about 4 marginal spines and small group of apical spines ; inner ramus equal to length of outer with only small group of apical spines. *Uropod* 2 peduncle with 3 marginal spines and small ventrodistal process ; outer ramus with 3 marginal spines ; inner ramus equal to length of outer with only small group of apical spines (occasionally small marginal spine present). *Uropod* 3 (Fig. 7e) peduncle elongate with single distal spine ; outer ramus with pair of large curved spines and finely denticulate dorsal margin ; inner ramus with small apical spine and about 5 long setae. *Telson* fleshy entire, with distinct distolateral hooks and several short dorsal setae.

DISTRIBUTION. This species is quite widely recorded in the north-east Atlantic area, although probably confused with *neglectus* over part of its range : coast of Europe from northern Norway (Vader, 1969, 1971), British Isles, to western Mediterranean, Azores and Canary Isles (Chevreux & Fage, 1925). It is possible that Chevreux & Fage confused *gammaroides* and *bicuspis*, and that *gammaroides* does not occur in the Mediterranean. The figured material was collected from the Shetland Isles.

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THE FIRST ZOEAL STAGE OF *SCOPIMERA CRABRICAUDA* ALCOCK (CRUSTACEA, BRACHYURA, OCYPODIDAE).

By A. L. RICE

ABSTRACT

The first zoeal stage of the ocypodid crab *Scopimera crabricauda* is described and compared with previously described larvae of the same family.

INTRODUCTION

RICE (1975) described the first zoea of *Macrophthalmus depressus* Rüppell and reviewed the available information on larval development within the brachyuran family Ocypodidae, pointing out that there seem to be clear differences between the zoeae of the three recognized sub-families, particularly in the setation of the mouthparts. However, knowledge of one of these sub-families, the Scopimerinae, is based on published descriptions of the larvae of only five species, belonging to three genera, and most of these accounts are very inadequate. Within the genus *Scopimera* only the first stage of *S. globosus* has been described (Aikawa, 1929) so that when first zoeae were obtained from female *S. crabricauda* collected in Bahrain, Arabian Gulf, a detailed description seemed desirable, even though all the animals died without moulting.

MATERIAL

Two ovigerous female *S. crabricauda* were collected from the foreshore at Jufair, Bahrain, in April 1975 and were maintained in aquaria in the laboratory of the adjacent Fisheries Resources Bureau at a salinity of 42‰ and a temperature of 19 °C until the larvae hatched some ten days later. Although the zoeae were supplied with freshly hatched *Artemia* nauplii, none of them moulted into the second stage.

The adults were fairly confidently identified as *S. crabricauda* since they agree quite well with Alcock's (1900) original description and Kemp's (1919) additional notes based on material from Karachi. Stephensen (1945) identified specimens from Bushire on the coast of Iran as *S. crabricauda*, but pointed out that the sculpturing on the dorsal surface of the carapace was much less pronounced than in the specimens from Pakistan. This sculpturing is similarly unclear in the Bahrain material and, in addition, the blunt ridge on the inner face of the chela seems to be less well developed than Kemp's description suggests. However, agreement in other characters is good, and the identity of the Bahrain animals with Alcock's species is supported by the presence in the same area of males which are apparently conspecific with the

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ovigerous females and which possess the racket-shaped abdomen so characteristic of *S. crabricauda*.

The adult female crabs, and the larvae obtained from them, are deposited in the collections of the British Museum (Natural History) under reg. nos 1976:71, 1976:72, 1976:73, 1976:74.

DESCRIPTION OF THE LARVAE

Dimensions. Carapace length (base of rostrum between the eyes to posterio-lateral carapace margin) 0·46–0·50 mm. Tip of dorsal to tip of rostral carapace spines 2·46–2·65 mm. Carapace width (tip to tip of lateral spines) 0·44–0·53 mm.

Carapace (Fig. 1a, b). Long dorsal and rostral carapace spines ; dorsal spine more than twice carapace length, rostral spine almost three times carapace length. Lateral carapace spines short and straight. Posterio-lateral carapace margins naked, but dorsal carapace surface with a pair of small setae anterior to the base of the dorsal spine.

Eyes. Fused.

Antennule. Unsegmented, with 2 terminal aesthetascs and one or two setae.

Antenna (Fig. 1a, b, d). Spinous process about $\frac{1}{3}$ length of rostrum, with a total of about 15 spinules becoming longer distally. No endopod or exopod.

Maxillule (Fig. 1e). Endopod 2-segmented ; proximal segment naked, distal with 4 terminal setae.

Maxilla (Fig. 1f). Endopod bi-lobed, with 3 and 2 setae respectively ; basal endite bi-lobed with 3 and 4 setae ; coxal endite weakly bi-lobed with a total of 5 setae. Scaphognathite with 4 marginal setae and a long, setose posterior process.

Maxilliped 1 (Fig. 1g). Basis with 10 medial setae arranged 2, 2, 3, 3 ; endopod of 5 segments with 2, 2, 1, 2 and 4+1 setae ; third segment with 2–6 very fine hairs on the lateral margin. Exopod with 4 natatory setae.

Maxilliped 2 (Fig. 1h). Basis with 3 medial setae ; endopod of 3 segments with 0, 1 and 6 setae respectively. Exopod with 4 natatory setae.

Abdomen (Fig. 1a, c). Somites 2 and 3 with small dorso-lateral process ; somites 3 and 4 with short posterio-lateral spines. Dorsal surfaces of somites 2–5 and of the telson with many very small spinules arranged in a more or less symmetrical pattern. Telson long and narrow ; forks long and divergent, each with a pronounced dorsal spine. Posterior margin with a deep median cleft and with 3 pairs of setae less than half the length of the forks.

DISCUSSION

The characterization on the basis of mouthpart setation of the larvae of the Scopimerinae as opposed to the other ocypodid sub-families, suggested by Rice (1975), is supported without change by this account of the first zoea of *S. crabricauda*.* This short discussion will therefore be restricted to the Scopimerinae.

Although the larvae of *S. crabricauda* resemble very closely Aikawa's (1929) description of the zoea of *S. globosus*, there are nevertheless clear differences between

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* The setation of the endopod of the maxillule in *S. globosus* is 0, 4, as in *S. crabricauda*, and not 0, 5 as given by Rice (1975) while a dorsal spine is present on each telson fork in both species.

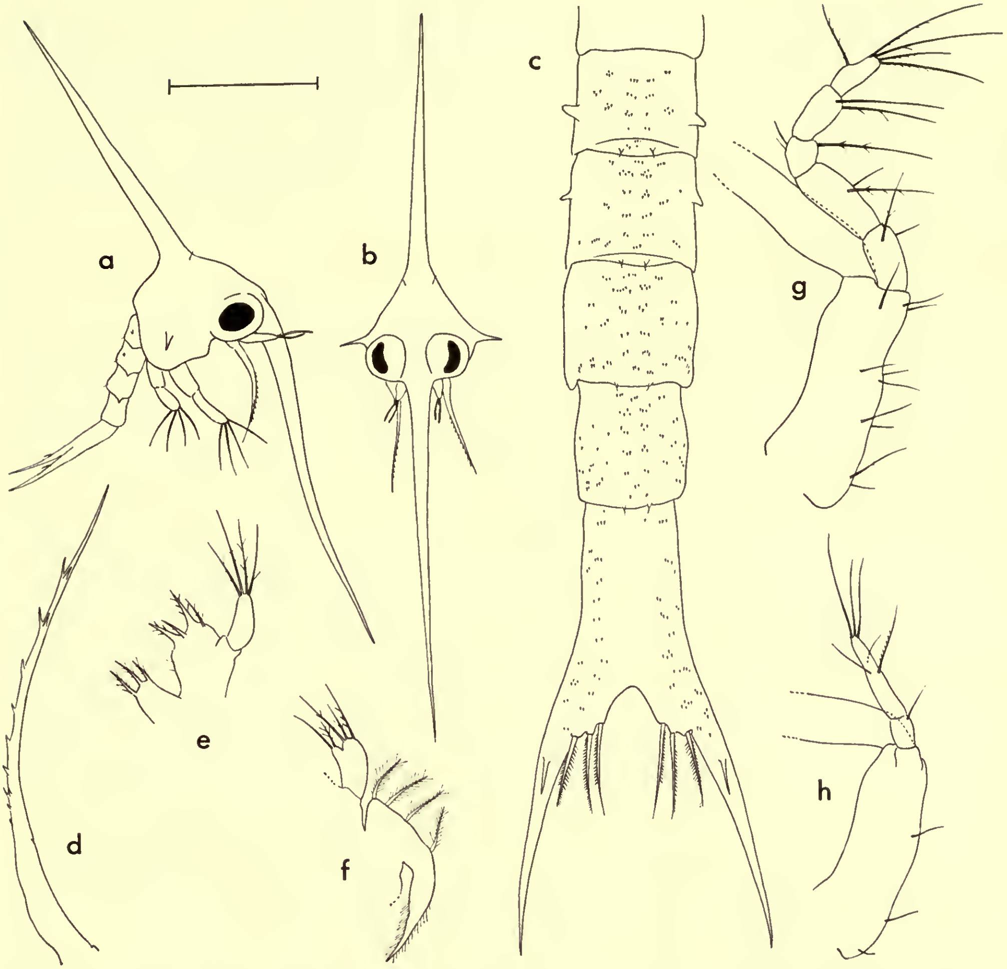

FIG. 1. *Scopimera crabricauda*, stage I zoea: (a) lateral view; (b) frontal view; (c) abdomen; (d) antenna; (e) maxillule; (f) maxilla; (g) first maxilliped; (h) second maxilliped. The bar scale represents 0·5 mm for a and b, and 0·1 mm for c–h.

the two species. First, the dorsal and rostral carapace spines are much longer in *S. crabricauda* (> twice carapace length) than in *S. globosus* (< twice carapace length). Second, these spines are completely naked in *S. crabricauda* whereas Aikawa describes them as 'sparsely toothed' in *S. globosus*. Finally, according to Aikawa's fig. 52, abdominal somites 3 and 4 in *S. globosus* lack the small but clear posterio-lateral spines present in *S. crabricauda*.

The available descriptions of the larval stages of other members of the Scopimerinae (see Rice, 1975) are not sufficiently detailed to enable generic characters within the sub-family to be discussed. Nevertheless, it seems that the zoeae of the three genera *Scopimera*, *Ilyoplax* and *Dotilla* may be distinguished between by the lengths of their dorsal and rostral carapace spines relative to the carapace length, these spines being longest in *Scopimera*, shorter in *Ilyoplax*, and shortest in *Dotilla*. This variation in carapace spine length is reflected in a difference in overall size, the first zoeae of *S. crabricauda* and *S. globosus* being more than 2 mm from the tip of the dorsal spine to the tip of the rostral spine, whereas in the described first stages of *Ilyoplax* and *Dotilla* species this dimension is little more than 1 mm. Finally, the wing-like expansions of the fifth abdominal somite in the zoeae of *Dotilla* species (see Ramadan, 1940; Gohar & Al-kholy, 1957; Rajabai, 1959) clearly distinguish them from the known larvae of both *Scopimera* and *Ilyoplax*.

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ASTEROZOA FROM AMSTERDAM AND ST PAUL ISLANDS, SOUTHERN INDIAN OCEAN

By AILSA M. CLARK

SYNOPSIS

Asteroids and ophiuroids collected recently around Amsterdam and St Paul Islands by French scientific collectors in association with lobster fishing vessels are reported. One new species of asteroid, a goniasterid named *Sphaeriodiscus mirabilis*, is described and the systematic position of another asteroid, named *Culcita veneris* by Perrier (1879) but now confirmed as better placed in *Spoladaster*, is discussed at some length with comments on related Poraniidae. Besides a third asteroid and one ophiuroid species previously recorded, four other ophiuroids new to these islands are also found to occur there.

INTRODUCTION

THE interesting collection of Asterozoa which forms the basis for this report was sent to the British Museum by Dr P. M. Arnaud of the Station Marine d'Endoume in Marseille. The material was primarily collected by Dr J. Beurois in 1971–72 but a few additional specimens originated from P. M. Arnaud, P. Noel, R. Vranckx, M. Segonzac and the fishing vessel *Maria Martina*.

Financial support for the collectors came from Terres Australes et Antarctique Françaises and logistic support from S.A.P.M.E.R. (Société Anonyme de Pêche Maritime et de Ravitaillement), to which institutions thanks are also due.

Hitherto the only published records of Asterozoa from these remote islands in the Indian Ocean (*c*. 38°S, 77½°E) were based on material from two sources. Firstly the French Transit of Venus Expedition, 1874–75 (naturalist C. Vélain), from which two asteroids, named as *Asterina exigua* (Lamarck) and *Culcita veneris* sp. nov., were reported by Perrier (1879). Secondly the German South Polar (*Gauss*) Expedition of 1901–3, which evidently took only the first asteroid, recorded as *Patiriella exigua* by Döderlein (1927), and one ophiuroid, recorded as *Amphipholis minor* by Hertz (1927). Dartnall (1971) confirmed that the *Gauss* asteroids are conspecific with *Patiriella exigua* (Lamarck) from South Africa and temperate Australia, when he split off tropical records of *P. exigua* as a distinct species. In contrast, Perrier's second asteroid and the new species now described appear to be endemic to these isolated islands.

Thanks to offshore work by lobster fishing vessels on the shelf around these islands to a depth of about 300 m and to painstaking collecting from washings of encrusting organisms, one fine new species of goniasterid starfish and four additional species of ophiuroids are included in the present material. Unfortunately most of the ophiuroids are very small and not in good condition and one amphiurid is not

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identifiable to species. However, the other three indicate an affinity with the ophiuroid fauna of south and south-east Africa in similar latitudes up-current in the West Wind Drift. This accords with the distribution of some other benthic invertebrates.

DESCRIPTION OF SPECIES

ASTEROIDEA

Sphaeriodiscus mirabilis sp. nov.

(Pls 1 and 2)

Material. Vicinity of St Paul and Amsterdam Islands at 200–300 metres, fishing vessel *Maria Martina*, 1971, the holotype, B.M. reg. no. 1976.1.12.1.

Description. R/r 70/45 mm = 1·56/1. The breadth of the swollen arm tip is c. 26 mm.

The area of abactinal plates is almost pentagonal. After preservation in spirit it is sunken below the raised rim of the superomarginal plates. Distally the abactinal plates are hexagonal and fairly regular in arrangement in longitudinal and diagonal series but interstitial plates are found proximally to about two-thirds R from the centre and as these become larger and more numerous towards the centre the regular arrangement is lost. A mid-radial row of plates is just discernible, though proximally its constituent plates are all separated. Conversely the plates of the interradial rows are nearly all contiguous.

All the plates are flat-topped and covered with a pavement of close polygonal flat-topped granules, numbering about 70 on the larger plates. Papulae are widespread except close to the superomarginals and in interradial bands.

The madreporite is triangular with two angles truncated to form an irregular pentagon. It lies at about one-third r from the centre.

The superomarginal plates number only four in each series (i.e. eight on each of the five sides) with the exception of one series where a short extra plate occurs between the second and third. In some of the other series at this same position a triangular abactinal plate is partially inserted between these two marginals, possibly reinforcing this vulnerable area. The two inner superomarginals are elongated tangentially, rectangular in outline and slightly raised at the joints, though in general with a part-cylindrical section. The third plate is abruptly enlarged and swollen, extended radially to meet its fellow ; together with the two smaller fourth superomarginals of each ray these make the upper side of a discrete broad rounded knob. The sutures between the third and fourth plates are oblique to the midradial line and the fourth plates are unequal in size so that the sutures are asymmetrical in all five cases.

The inferomarginals match the upper series in general but individual plates may be slightly misaligned ; also there is an additional fifth plate in each series, bordering the small spout-like terminal plate. The third to fifth plates participate in the knob-like expansion of the tip. The more convex areas of the swollen marginals are mostly naked with only scattered granules over most of their surface and these sunk into sockets in the plates ; only peripherally is the granulation continuous, as it is on the first two (interradial) plates. The suture between the two marginal series is distinctly above the ambitus so that the inferomarginals are clearly visible from above but this may be due to contraction of the upper side during preservation.

The actinal plates in the distal halves of the rays form regular longitudinal series but proximally the arrangement becomes irregular because of the development and enlargement of interstitial plates. All the plates are fully covered with polygonal flat-topped granules distinctly coarser than the abactinal ones with the peripheral row discrete, even to the naked eye.

The adambulacral plates mostly bear five short blunt-tipped furrow spines, aligned vertically, sometimes four or (distally) six. These stand out slightly from the lower surface but are backed by several series of shorter 'spines' transitional to granules, all angular in section.

No pedicellariae can be distinguished.

AFFINITIES. This handsome goniasterid with its limited number of marginal plates has a considerable resemblance to those individuals of *Pentagonaster pulchellus* Gray, from temperate Australasia, with swollen arm tips (such as the holotype shown in Gray's pl. 8, fig. 3, 1866). *Pentagonaster* differs however in having the abactinal plates with only peripheral granules and their centres more or less markedly convex ; also the individual marginal plates are rounded at the angles, not rectangular. There is also a remarkable resemblance to the Jurassic *Miopentagonaster calloviensis* Mercier in the very broad rounded arm tips, though again in that fossil species it is only the distalmost marginal of each series (together with the enlarged terminal plate in this case) that forms the expansion. The interradial marginals of *M. calloviensis* number only four on each of the five sides and appear rectangular in dorsal view, as in *S. mirabilis.*

However, judging from the great variation in the breadth of the arm tips in various goniasterid species such as *Pentagonaster pulchellus* and *Tosia australis* I think it likely that other specimens from the Amsterdam/St Paul area may prove to have more pointed arm tips. This is the case in the holotype of *Sphaeriodiscus scotocryptus* Fisher, 1913, from the Philippine Islands. It too has an almost complete granule covering, except on the centres of the marginal plates, a basically pentagonal form but for projecting tips to the rays and a limited number of marginal plates – in this case at R 32 mm five superomarginals with the three rectangular proximal ones of each series forming the sides of the body and the two distal ones contiguous midradially with their corresponding plates and forming the arm tip. Apart from these narrow arm tips and the additional marginal plate in each series at a smaller total size, *S. scotocryptus* differs from the new species in having seven to ten furrow spines on each plate, besides numerous pedicellariae, though this last may not be a specific character.

Of the other species of *Sphaeriodiscus*, the type species, *Sphaeriodiscus bourgeti* (Perrier, 1885) from off north-west Africa, also has four superomarginals but the first one is relatively short (tangentially) and the second is distinctly more swollen though not meeting its fellow midradially, the third plate is still convex but smaller than the second so that the outline is approximately pentagonal. The largest of Perrier's specimens had R 35 mm. H. L. Clark (1926) has recorded a specimen with R 27 mm from off Natal in 420 m as *S. bourgeti*, expressing surprise about the extension of range to the south-*east* side of South Africa. The fourth superomarginals are only just beginning to appear and the arm tips are somewhat swollen, vertically if not horizontally, at least, judging from the measurements. He compared it with a syntype and with Perrier's figures and found no significant difference, so the Natal specimen presumably also has the second superomarginal distinctly larger and more swollen than the first, a condition also found by Madsen (1958) in a specimen of *S. bourgeti* from the Cape Verde area and difficult to reconcile with the close similarity of the first two marginals in *S. mirabilis*. Madsen compared *S. bourgeti* with a small specimen of *S. placenta* (Müller & Troschel, 1842), known from widespread localities in the Atlantic and Mediterranean, the main difference in the latter being the similarity of the consecutive superomarginals of which the fourth is already well developed. *S. placenta* is known to reach a size of nearly 90 mm R and at the same time to increase the number of marginals in each series to a maximum of nine superomarginals, though more often five to seven ; two to five of the distal ones may be contiguous midradially and the arm tip may be broadened in some specimens as shown in Tortonese's fig. 72 (1965) of a Mediterranean example.

In the Pacific, *Sphaeriodiscus inaequalis* (Gray, 1847), supposedly from Amboina or New Guinea, has an even more diminutive first marginal in both upper and lower series than *S. bourgeti* in comparison with the second and third plates, which are markedly elevated with more or less tabulate raised areas, also on the corresponding inferomarginals, though at the same time the arms taper to a blunt point since the distal superomarginals are hardly at all expanded horizontally. At R only 21 mm, as in the holotype and only recorded specimen, there are only three or four superomarginals in each series. Owing probably to abrasion of the surface, this specimen does not show the characteristic 'peppered' appearance of the barer parts of the marginals of *Sphaeriodiscus* due to the recessed isolated granules, but this appearance is very conspicuous in Fisher's photograph (1906) of the holotype of *Sphaeriodiscus ammophilus*, from the Hawaiian Islands. At R only 24 mm this has but three superomarginals and the third is relatively small yet, though the first is hardly at all smaller than the second. The form is pentagonal.

LOCALITY. Unfortunately a small element of doubt exists concerning the type locality of *S. mirabilis*. Although the specimen came to Dr Arnaud together with invertebrates characteristic of the shelf in the vicinity of Amsterdam and St Paul Islands at 200–300 metres, the *Maria Martina* had also worked off South Africa and Réunion Islands. If it should prove that specimens of *Sphaeriodiscus* from Natal are conspecific with *S. mirabilis* rather than with *S. bourgeti* and no further material from these two remote islands is forthcoming, then the species may have to be deleted from their fauna.

Patiriella exigua (Lamarck, 1816)

Psterias exigua Lamarck, 1816 : 554.
Asterina exigua : Perrier, 1879 : 47.
Aatiriella exigua : Döderlein, 1927 : 296 ; Dartnall, 1971 : 40–43, pl. 4, fig. c.

Material. Amsterdam Island: mostly from the north side in the vicinity of La Roche Godon, under or on mid- or sub-littoral stones or in pools at low water, 60 specimens.

St Paul Island: from the crater, mostly the north-east part near the entrance, on or under sub-littoral or sometimes mid-littoral stones or from scrapings, usually with white or green algae, ascidians or sponges and often with *Amphipholis squamata* and *Amphiura capensis*, 111 specimens.

Notes. Of the total of 171 specimens, two are four-rayed and two are six-rayed. Six out of 48 specimens from Beurois' station St Paul 8a (from the north-east part of the crater among lower mid-littoral and sub-littoral stones) appear more or less deformed, one having abnormally short rays and the interradii convex, making an ovate outline; the other five have one or sometimes two rays aborted or possibly regenerated, their other four (or three) rays aligned at right angles to each other. The smallest specimens have R *c.* 0·5 mm and three pairs of tube feet in each ray.

Spoladaster veneris (Perrier)

(Fig. 1; Pl. 3, figs 1, 2; Pl. 4, figs 1, 2; Pl. 5, figs 1, 2; Pl. 6)

Culcita veneris Perrier, 1879: 47–49, pl. 4; Mortensen, 1933: 249, 250; Arnaud & Beurois, 1972: 874 [Non *C. veneris*: Bell, 1905: 248.]
Spoladaster ? *veneris*: Fisher, 1940: 136; A. M. Clark, 1952: 208.

Material. Amsterdam Island: off east coast at 'BMG', in lobster pot, depth unknown, possibly 10–50 metres, with gastropods *Ranella olearium* and *Charonia lampas pustulata*, 1 specimen; no details, 1 specimen; from washings of the large bryozoan *Turbicollopora redoutei*, sponges, gorgonians, the scleractinian coral *Caryophyllia profunda*, alcyonarians, etc. at 80–100 metres, 1 juvenile.

St Paul Island: off east coast in lobster pots, *c.* 300 metres, 3 specimens; north-west coast at La Chaussée du Phoques, 10–50 metres ?, 2 specimens; near Roche Nord, in lobster pot, 1 specimen; various parts of the crater (the type locality) at 0·5–1·0 metre and in sublittoral scrapings, sometimes with the gastropods *Ranella* and *Charonia* and with echinoids, 5 specimens.

Description. A photograph of a live specimen (Pl. 6, fig. 1) shows a distinctly stellate form, R/r *c.* 1·8/1, whereas the preserved specimens all appear more nearly pentagonal with R/r 1·2–1·5/1. There must therefore be considerable contraction across the interradii marginally in preservation, possibly correlated with bending upwards of the arm tips, the resultant form having a close superficial resemblance to a *Culcita*. The collectors of Perrier's type material noted a considerable ability of the live animals to vary the shape of their outlines and degree of inflation of the upper side, which was also noted by the recent collectors. When inflated the whole appearance is said to be very like an orange, with which the bright colour of the upper side also agrees; the lower side is paler. In the live specimen photographed the madreporite shows up clearly about midway from the centre to the indented interradial edge but in preserved specimens it appears at a quarter to a third r from the centre. The enlargement of an arm in life (Pl. 6, fig. 2) shows a very 'shaggy' effect produced by the extended papulae, which appear to arise all over the upper side except for narrow bands, notably in the interradii and in the centre, with only the slightest indication of grouping as in the meshes of a reticulum. In specimens preserved in alcohol the papulae are more or less retracted. A rough texture can be felt through the pustular skin, produced by numerous fine spinelets, which are invisible unless the specimen is partially or completely dried. These are isolated in the body wall, not based on skeletal plates. Indeed, X-radiography of an adult shows that the only abactinal plates of any density remaining are a few at the tips of the rays. The spinelets have the shape shown in Fig. 1(a). On the upper surface the spinelets are fairly evenly scattered but on the sides of the body they tend to become aligned in vertical series. At the junction of abactinal and actinal areas below the ambitus, where the papulae cease abruptly, this linear arrangement is even more marked and the pustular skin covering forms folds with narrow grooves between leading to the adambulacral furrows. Some of these series branch or anastomose.

In wet specimens there is usually a distinct change in the contours where the actinal and abactinal areas meet, with a slight horizontal ridge where one would expect to find the inferomarginal series of plates. Drying tends to emphasize this and may bring out a second apparently reinforced band just above. However, there is no trace of a separate intermarginal band of papulae, such as occurs in *Porania*. X-radiographs show no marginal plates at all (Pl. 5, figs 1, 2), nor do drying, dissolving the body wall or xylol treatment reveal any vestiges of marginal plates, even viewing from the inside of the body wall (Pl. 3, fig. 1), except at the tips of the rays. The external change in contours must therefore be due to reinforcing bands of connective or muscle tissue.

The actinal spinelets are similar in form to the abactinal ones and are similarly isolated in the body wall. The X-radiographs taken fail to show up any actinal plates but special treatment or viewing from inside reveals that in each V-shaped interradial area adjoining the oral plates and the proximal adambulacrals is a small triangular patch of hollow, extremely thin-walled, rounded actinal plates (Fig. 1c). More distally there are traces of two, possibly three, partial series of plates running parallel to the inferomarginal series but these are not complete interradially in any of the areas treated and usually only the youngest plates adjoining the adambulacral plates are at all distinct. Presumably these actinal plates are progressively reduced during growth. None of these vestigial plates bear any enlarged spinelets or spines.

The adradial ends of the actinal pustular folds envelop the subambulacral spines as well ; these number two on one or two proximal plates but one on the rest. There are two separately sheathed spines bordering the furrow on most plates. The oral plates usually have four furrow spines and one larger subambulacral spine, though larger specimens, R 60+ mm, may have two.

The juvenile specimen (Fig. 1g, h) has R/r 1·5/1·3 mm (excluding the length of the marginal fringe of spinelets). The margin is formed entirely by the relatively large inferomarginal plates, four on each of the five sides, and the terminal plates. The adjacent plates dorsally (presumably superomarginals) are markedly convex at their outer edges. There are two midradial plates on each ray and a ring of five larger primary interradial plates around a small central area including the anus. All these

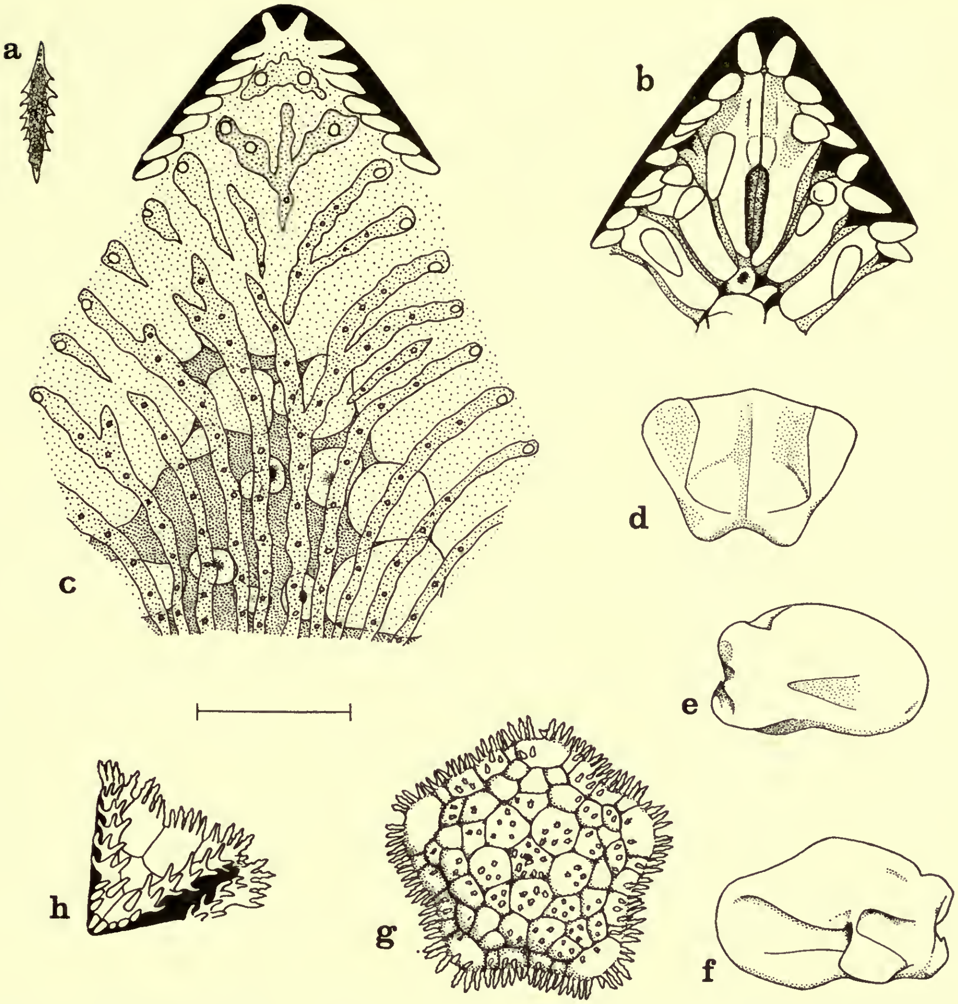

Fig. 1. *Spoladaster veneris* (Perrier). (a–f) St. AMS-104. R *c.* 55 mm. (a) Abactinal spinelet. (b) Jaw and adjacent four adambulacral plates, denuded except for major spines. (c) Proximal apex of one ventral interradius partly dried and cleared with xylene to show pustular folds (somewhat shrunken) with isolated spinelets and underlying reduced actinal plates. (d) Odontophore, viewed ventrally. (e, f) An isolated proximal adambulacral plate from the left side of a ray in aboral and adoral views, the furrow spines arose opposite the letter 'f' (g, h) St. AMS-96. Juvenile partly dried (some abactinal spinelets probably lost). (The scale equals *c.* 1 mm for a, *c.* 4 mm for b and c, *c.* 3 mm for d–f and 2 mm for g and h.)

plates bear spaced rugose spinelets, mostly about three times as long as broad and slightly waisted. On the inferomarginals the spinelets graduate to the horizontal fringe of spinelets bordering the entire animal, which is interrupted only at the distal ends of the furrows. The ventral side is quite flat. The inferomarginals are completely naked ventrally and the two first ones in each interradius cover most of the interradial area together with the single actinal plate proximal to them. Two of the five actinal plates bear a single median distal spinelet but the other three are completely bare. There are six pairs of podia in each ray. Except for the first plate, the adambulacrals bear three spines in a more or less straight line at right angles to the furrow. The first plates may have four spines, the second one aligned obliquely to the first and clearly potentially a furrow spine. Presumably during further growth the second spine on the succeeding plates also shifts to the furrow edge of the plate. The oral plates already have four furrow spines and one suboral, as in most adults.

The general appearance of this specimen is remarkably like the holotype of *Marginaster fimbriatus* Sladen, 1889, as shown in Sladen's pl. 58, figs 4–6 ; that has R 6 mm and was collected to the north of Ireland. According to Ludwig it is conspecific with *Marginaster capreensis* from the Mediterranean but I consider that its affinities are much more likely to be with *Poraniomorpha*. The only difference between *M. fimbriatus* and this juvenile from the Indian Ocean is the development of a second row of actinal plates, which would be expected at the larger size.

There is no question that this small specimen could be a young *Patiriella exigua* since there are examples of that species of comparable size and they show a much more granuliform armament, with single shorter adambulacral spines. Also the contours are quite different, the abactinal side rising vertically above the relatively smaller and more numerous inferomarginal plates.

GENERIC POSITION. Perrier described this species as belonging to a separate section of the genus *Culcita* (now included in the tropical shallow-water family Oreasteridae of the order Valvatida), this section being characterized by the fleshy body wall concealing the skeleton. He also noted affinities with *Asteropsis* (currently aligned near the Poraniidae in the order Spinulosida).

In 1905 Bell identified a fleshy pentagonal South African asteroid as *Culcita veneris* but Mortensen (1933) referred this specimen to *Cryaster brachyactis* H. L. Clark, 1923, also from South Africa. At the same time Mortensen pointed out that *Culcita veneris* is not a *Culcita* but probably belongs to the Asteropidae or perhaps the Cryasteridae, though in a footnote he doubts the distinction of these two nominal families.

In 1940 Fisher demonstrated that *Cryaster antarcticus* Koehler, 1906, the type-species of that genus, is congeneric with *Perknaster fuscus* Sladen, 1889 and so referable to the family Ganeriidae. However, he recognized that this affiliation does not extend to *Cryaster brachyactis*, for which he established a new nominal genus *Spoladaster*, referring it to the Asteropidae 'in the vicinity of *Tylaster*'. On the strength of Mortensen's comments, Fisher noted that *Culcita veneris* can probably also be referred to *Spoladaster*, an idea shared by me in 1952, when I suggested also that the South African *Tylaster meridionalis* Mortensen, 1933 might be based on smaller specimens of *Spoladaster brachyactis*. If this last premise proves true, then the problem is whether the species from South Africa and from Amsterdam and St Paul Islands are congeneric with *Tylaster willei* Danielssen & Koren, 1881, from the deep Norwegian Sea, this being the type species of *Tylaster*.

More immediately there is still a possibility that specimens from Amsterdam and St Paul Islands could be conspecific with those from South Africa, in spite of

Mortensen's denial of this (probably without seeing specimens from the islands). Zoogeographically this would be quite likely in view of the fact that *Patiriella exigua*, one of the two other asteroids known from these isolated islands, is also found in southern Africa, though it occurs also in temperate Australia. In addition, at least two species of ophiuroids, as well as the cosmopolitan *Amphipholis squamata*, are here recorded as common to this island group and to either South Africa or southern Mozambique.

However, the specimen of *Spoladaster brachyactis* in the British Museum collections from False Bay shows a distinct grouping of abactinal papulae in the meshes of an irregular reticulum, as described by H. L. Clark in the holotype. Also there is a separate horizontal band of papulae laterally in what should be the intermarginal area (Pl. 3, fig. 3, top). H. L. Clark describes 'innumerable minute' abactinal plates bearing the spinelets in the holotype, though Fisher found in the paratype that abactinal plates of any sort are only present at the arm tips and I am unable to find such plates in the general abactinal body wall either. H. L. Clark also describes a series of 'rather large plates buried in the skin' between abactinal and actinal areas, i.e. inferomarginal plates, while Fisher found that the paratype has 'fairly large phanerozonid inferomarginal plates imbedded in the leather body wall'. However, the X-radiograph taken of the British Museum specimen shows no trace of any marginal plates (Pl. 5, fig. 3), though the external view (Pl. 4, fig. 3) shows that some short inferomarginal spines are present. Unfortunately this is the only South African specimen now in the British Museum collections and I hesitate to mutilate it further to ascertain if any rudiments of marginal or actinal plates, as described by Fisher, are visible on the inside of the body wall. In Mortensen's smaller holotype of *Tylaster meridionalis* from South Africa with R 28 mm there is a continuous marginal fringe of short spines, with a parallel series of a few similar actinal spines close by on the distal part of each actinal area mid-interradially. In another specimen (presumably of similar or smaller size since it was not selected as holotype) which he dried, Mortensen made visible three or four irregular series of actinal plates. The Cape Town University specimen with R *c.* 80 mm which I referred to *Spoladaster brachyactis* in 1952 has numerous actinal spines, which would be much coarser than the microscopical actinal spinelets of the Amsterdam/St Paul material. Finally, the adambulacral plates of *S. brachyactis* (and of *Tylaster meridionalis* – if distinct) bear only one furrow spine apart from the subambulacral spine, whereas the Amsterdam/St Paul specimens have two furrow spines. I have no doubt therefore that the latter specimens are specifically distinct, so that *S. veneris* is a species endemic to the islands.

The differences can be summed up as follows :

Spoladaster veneris	*Spoladaster brachyactis*
No separate intermarginal band of papulae laterally	An intermarginal band of papulae distinct
No enlarged spines at the junction of the abactinal and actinal areas, nor on the actinal areas	Some inferomarginal spines usually present and in smaller specimens (R *c.* 35 mm) also some actinal spines
Two furrow spines on most adambulacral plates	Furrow spines usually single

The problem remains as to whether or not these two species should be regarded as congeneric with one of the northern hemisphere genera such as *Tylaster* or *Poraniomorpha*, both of Danielssen & Koren, 1881.

Unfortunately only a single young specimen of *Tylaster willei* is in the British Museum collections. This is the smaller specimen from Norwegian North Atlantic Expedition station 200 (71°25'N ; 15°41'E, 1134 metres). It has R only *c.* 12 mm. The triangular arms are curled up dorsally but the form is markedly stellate rather than pentagonal. There are prominent inferomarginal and actinal spines similar in size to the adambulacral spines. The species was very well described by Danielssen & Koren in 1884 (pp. 64–67, pl. 11, figs 1–6), presumably on the basis of the single larger specimen, which was from the same station as this one. R is given as 40 mm and R/r can be calculated as 1·6/1, the form again being markedly stellate. Drying of the dorsal body wall revealed numerous isolated spinelets, described as needle-like but appearing to be quite capitate in their pl. 11, fig. 3. Viewing the body wall from the inside showed a horizontal series of rudimentary isolated lateral plates which were assumed to be the superomarginals and below these three series of more regular small plates linked by connective tissue, also approximately horizontal, the upper one of the three being taken for the inferomarginals and bearing externally a horizontal series of marginal spines in groups of usually three corresponding to the plates. Many of the actinal plates also bear similar but single spines forming several series, while there are some scattered additional proximal actinal spines.

Tylaster willei thus seems intermediate in form and skeletal development between the *Spoladaster* spp. and the wide-ranging genus *Porania*, the latter having a usually stellate form and an articulated skeleton.

Not surprisingly, the Amsterdam/St Paul species is remarkably similar to some North Atlantic pentagonal cushion-like specimens which were likewise ascribed to *Culcita* under the name *Culcita borealis* Sussbach & Breckner, 1911, from the area of the Shetlands, which name Farran (1913) also gave to some specimens from the west of Ireland. In 1914 Verrill established a new nominal genus *Culcitopsis* for *C. borealis*, pointing out that its affinities are with *Tylaster* and *Chondraster* of the family Poraniidae (which he kept distinct from the Asteropidae).

Östergren (1904), Grieg (1907) and Koehler (1909) emphasized that *Poraniomorpha hispida* (M. Sars *in* G. O. Sars, 1872) is a very variable species, Koehler including records from both sides of the Atlantic in his lengthy synonymy. In 1927 Grieg referred *Culcitopsis borealis* to the synonymy of *P. hispida* and Mortensen (1927) agreed that 'there is hardly any doubt' this is correct. Most subsequent workers have accepted Mortensen's judgement so that the synonymy of this species includes the following :

Goniaster hispida M. Sars *in* G. O. Sars, 1872 : 28 (R of the holotype 11 mm) : Storm, 1881 : 90.
Asterina borealis Verrill, 1878 : 213 (R 12 mm).
Porania spinulosa Verrill, 1879 : 202 (R 40 mm).
Poraniomorpha rosea Danielssen & Koren, 1881 : 189 (R *c.* 27 mm, judging from the scale of the figures).
Rhegaster murrayi Sladen, 1883 : 156 ; 1889 : 368 (R 14·3 mm).
Lasiaster villosus Sladen, 1889 : 372 (R 10·5 mm).

Poraniomorpha hispida : Östergren, 1904 : 615 ; Koehler, 1909 : 100 ; Grieg, 1927 : 129 (with forma *borealis* Sussbach & Breckner) ; Mortensen, 1927 : 92.
Poraniomorpha (*Lasiaster*) *hispida* : Grieg, 1907 : 40.
Culcita borealis Sussbach & Breckner, 1911 : 217 (R 40 mm) ; Farran, 1913 : 15.
Poraniomorpha villosa : Farran, 1913 : 17.
Culcitopsis borealis (Sussbach & Breckner) Verrill, 1914 : 21.
Rhegaster borealis (Verrill) Verrill, 1914 : 17.

As shown by the R measurements for the holotype of each nominal species included above, most of them are based on relatively small specimens, the exceptions being *Porania spinulosa, Poraniomorpha rosea* and *Culcita borealis.* This is very unfortunate since small specimens of poraniids may give an exaggerated impression of the extent of skeletal development in the adult, as the evidence suggests there is often a tendency for progressive resorption with growth. It is significant that there are several other North Atlantic poraniids with markedly reduced skeletons, namely *Chondraster grandis* (Verrill, 1879), *Chondraster hermanni* Madsen, 1959 (treated as a subgenus of *Porania*), *Pseudoporania stormi* Dons, 1936, *Sphaeraster berthae* and *Sphaeraster björlykkei* Dons, 1938 – the last nominal genus preoccupied and subsequently renamed *Sphaeriaster* by Dons, all based on relatively huge specimens with R at least 80 mm and often 100 mm or even more. Madsen (1959) considers that all these are congeneric. I believe that their large size is responsible at least in part for their very reduced skeletons. The X-radiographs given by Dons and Madsen indicate that their material completely lacks abactinal and actinal plates of any substance and only Dons' *Pseudoporania stormi* has vestiges of supero- and inferomarginal plates.

The holotype of *Poraniomorpha hispida* is described as pentagonal in form, R/r 1·2/1, flat below and convex above, with both marginal series of plates distinct (probably by their contours). It came from the Lofoten Islands, off northern Norway. A larger specimen, R 40 mm, from Trondheim Fjord further south, presented to the British Museum by Storm, agrees well with this description (Pl. 3, fig. 4 ; Pl. 4, fig. 4 ; Pl. 5, fig. 4). It was X-radiographed for comparison with *Spoladaster brachyactis* and *S. veneris*, revealing very well-developed series of block-like supero- and inferomarginal plates outlining what appears to be an almost continuous pavement of slightly spaced plates, apparently mainly actinal plates but probably also some superimposed abactinals. In contrast, a cushion-like specimen in the British Museum collections, from the warm area of the Faeroe Channel, halved and dried (Pl. 4, fig. 5) shows only vestigial microscopic abactinal platelets on the inside of the body wall, small isolated superomarginals barely distinguishable interradially, slightly less reduced but still discontinuous inferomarginals and two well-separated series of isolated actinal plates with a group of additional proximal ones in each area. The inferomarginals and actinals are clearly in process of resorption, most of them being crescentiform or ring-shaped.

This degree of skeletal reduction approximates to that shown by *Spoladaster* and at the same time makes it difficult to regard *C. borealis* as conspecific with well-calcified specimens of *Poraniomorpha hispida* such as the one from Trondheim Fjord. Although he did not mention *Poraniomorpha* in his 1959 paper, Madsen's remarks on the variations of the northern *Porania pulvillus* suggest that the distinction between that and *Poraniomorpha* is by no means sharp and needs further study, especially of growth changes. Until this can be done for the northern poraniids and the various taxa can be redefined, it seems unwise to alter further the nomenclature of these two southern species, which I accordingly propose to leave under the name of *Spoladaster*.

OPHIUROIDEA

Amphipholis squamata (Delle Chiaje, 1829)

Asterias squamata Delle Chiaje, 1829 : 74, 77, figs 1–4.
Amphipholis minor : Hertz, 1927 : 35.
Amphipholis squamata : Mortensen, 1933 : 364–365.

Material. Amsterdam Island : mostly from mid- to sub-littoral, in algae or coralligenous substrates or rock pools from various parts of the shore, some from grab hauls off the east coast down to 80 metres, others from stomachs of fishes such as *Acantholatris monodactylus*, 135 specimens.

St Paul Island : from washings of algae and *Laminaria* roots, east coast towards Roche Quille, 3–4 metres, 24 specimens ; washed from *Macrocystis* roots, 62 specimens ; from various parts of the crater, mostly under sublittoral stones or in washings from sponges, algae, bryozoa, compound ascidians, etc., 150 specimens.

Sea-mount south-east of St Paul Island : with compound ascidians, the scleractinian coral *Caryophyllia profundi* and bryozoa at 120 metres, 1 specimen.

Notes. Most of these specimens are very small and in poor condition. Some were mixed with *Amphiura capensis* and also with young *Patiriella exigua*.

Mortensen has already pointed out that the *Amphipholis* from St Paul Island crater recorded by Hertz are not distinguishable from *A. squamata*, the only cosmopolitan echinoderm.

Amphiura capensis Ljungman, 1867

Amphiura capensis Ljungman, 1867 : 320 ; Mortensen, 1933 : 348–350.

Material. Amsterdam Island : washed from coralligenous bottom at 35 metres, north-east coast, 1 specimen ; from stranded laminarians, near La Cale, north coast, 3 specimens.

St Paul Island : from *Macrocystis* and *Laminaria* roots, 23 specimens ; from various parts of the crater, usually under sublittoral stones, 29 specimens.

Notes. Most of the specimens from the crater of St Paul Island were taken with *Amphipholis squamata* and some also with young *Patiriella exigua*. All are small, the disc diameter not exceeding 4 mm. The arm spines number up to five proximally and are markedly flattened and spatulate. Some specimens have the disc scaling deficient near the oral shields, as shown also in many South African specimens.

This species is easily distinguished from *Amphipholis squamata* by the radial shields being only contiguous distally, the arm spines being more numerous and a different shape and the distal oral papillae and tentacle scales being single.

These records represent an extension of range from southern Africa, where *Amphiura capensis* is known from Luderitz Bay to Natal.

Amphiura sp.

MATERIAL. St Paul Island : on coarse sandy bottom with *Venus* at 50–80 metres off the north-east coast, 4 specimens.

Sea-mount south-east of St Paul Island : with compound ascidians, *Caryophyllia* and bryozoa at 120 metres, 2 specimens.

NOTES. Unfortunately all these specimens are in poor condition. The disc was probably fully scaled, the radial shields about a third as long as the disc radius and contiguous for their distal third, inwardly divergent. The oral shields are as long as broad or slightly longer, with the distal lobe shorter than the proximal angle. The distal oral papilla is blunt. The dorsal arm plates are fan-shaped. There are four tapering but blunt-tipped arm spines. The tentacle scales mostly number two but one specimen has more pores with only a single small scale. None of these characters are particularly distinctive.

This species does not agree with any so far recorded from southern Africa, judging from these specimens.

Ophiactis sp. probably ***O. savignyi*** Müller & Troschel, 1842

MATERIAL. Amsterdam Island : dredged on consolidated bottom at 40–50 metres off north coast, 1 specimen.

St Paul Island : washed from various coralligenous encrusting organisms, compound ascidians, *Caryophyllia*, bryozoa, etc. at 60–80 metres off the north-east coast, 1 specimen.

NOTES. Both specimens are fissiparous with six arms ; one has three arms larger and three regenerating, the other has two and four.

Even the larger specimen has the disc diameter only just exceeding 1 mm. The disc scales are relatively coarse at this small size and the proportions of the radial shields not obvious – partly due to the regeneration. One specimen has disc spines, the other has not. Some of the jaws have two distal oral papillae on at least one side, elsewhere there is only one distinct papilla. The dorsal arm plates are fan-shaped but the distal curve is flattened medially. There are four rugose arm spines, all but the uppermost one truncated.

The occurrence of two distal oral papillae in some cases and the shape of the arm spines make it almost certain that these two small specimens are referable to the 'tropicopolitan' *Ophiactis savignyi*, which ranges down the coast of East Africa to Natal.

Ophiocoma pusilla (Brock, 1888)

Ophiomastix pusilla Brock, 1888 : 499.
Ophiocoma pusilla : Devaney, 1970 : 25–28.

MATERIAL. Amsterdam Island : on consolidated bottom at 40–50 metres off the north coast, 1 specimen.

Sea-mount south-east of St Paul Island : with compound ascidians, *Caryophyllia* and bryozoa at 120 metres, 10 specimens.

NOTES. The largest specimen has disc diameter 7·5 mm and is the only one to show the swollen-tipped arm spines on a few segments beyond the arm bases so characteristic of this diminutive species of *Ophiocoma.*

The granulation of the disc distinguishes this from any of the other species recorded from these two islands.

Ophiocoma pusilla is known from isolated records throughout the tropical Indo-West Pacific, as far south in East Africa as Inhaca, southern Mozambique. It is usually found in coral heads, mostly in shallow water but possibly down to just over 100 metres. Because of its furtive habits and likelihood of confusion with other species of *Ophiocoma*, it may well have been overlooked at greater depths.

One of the two localities at which this species was collected is common to the *Ophiactis* discussed above. If this really is *Ophiactis savignyi*, as seems very likely, then the extension of range to Amsterdam and St Paul Islands of another tropical reef species is not surprising.

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PLATE 1

Sphaeriodiscus mirabilis sp. nov. Holotype in dorsal view (scale in mm).

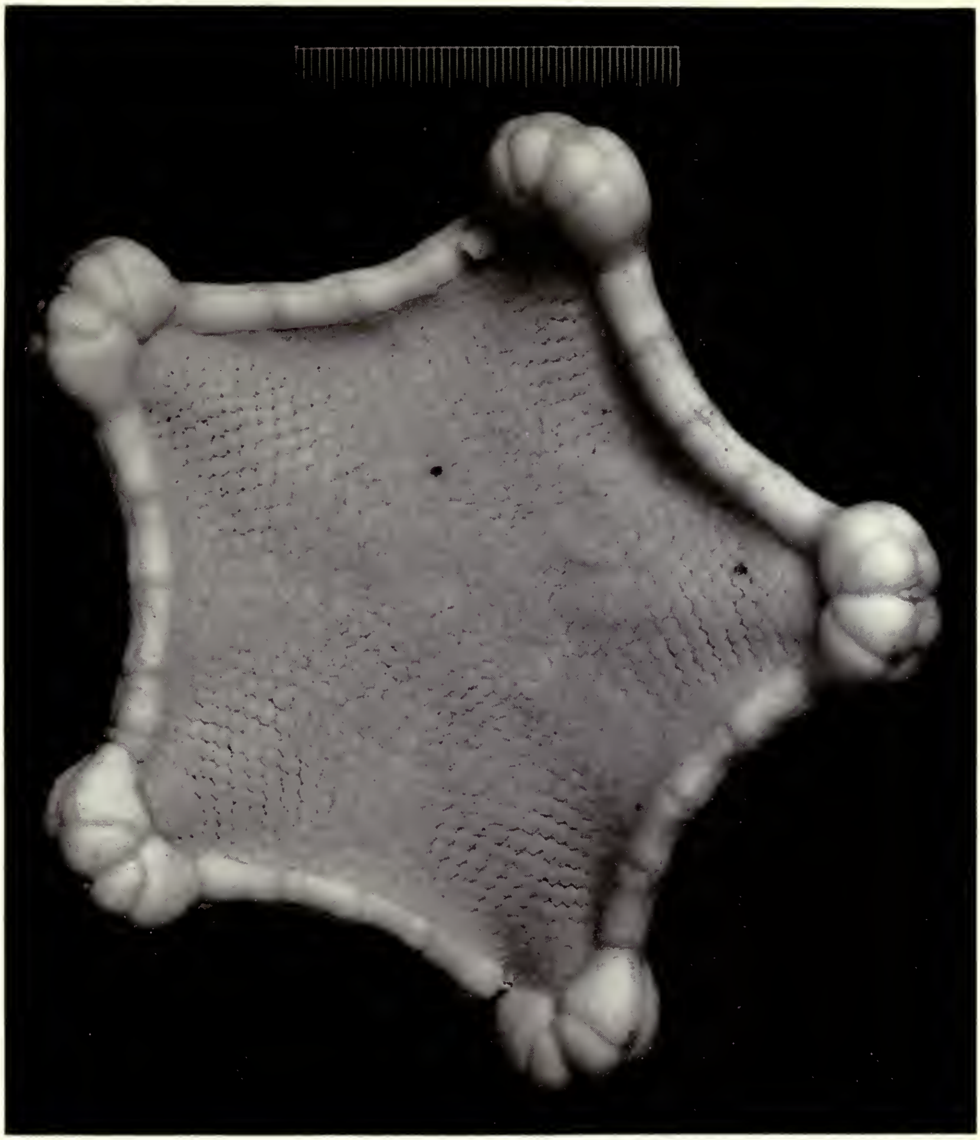


PLATE 2

Sphaeriodiscus mirabilis sp. nov. Holotype in ventral view (scale in mm).

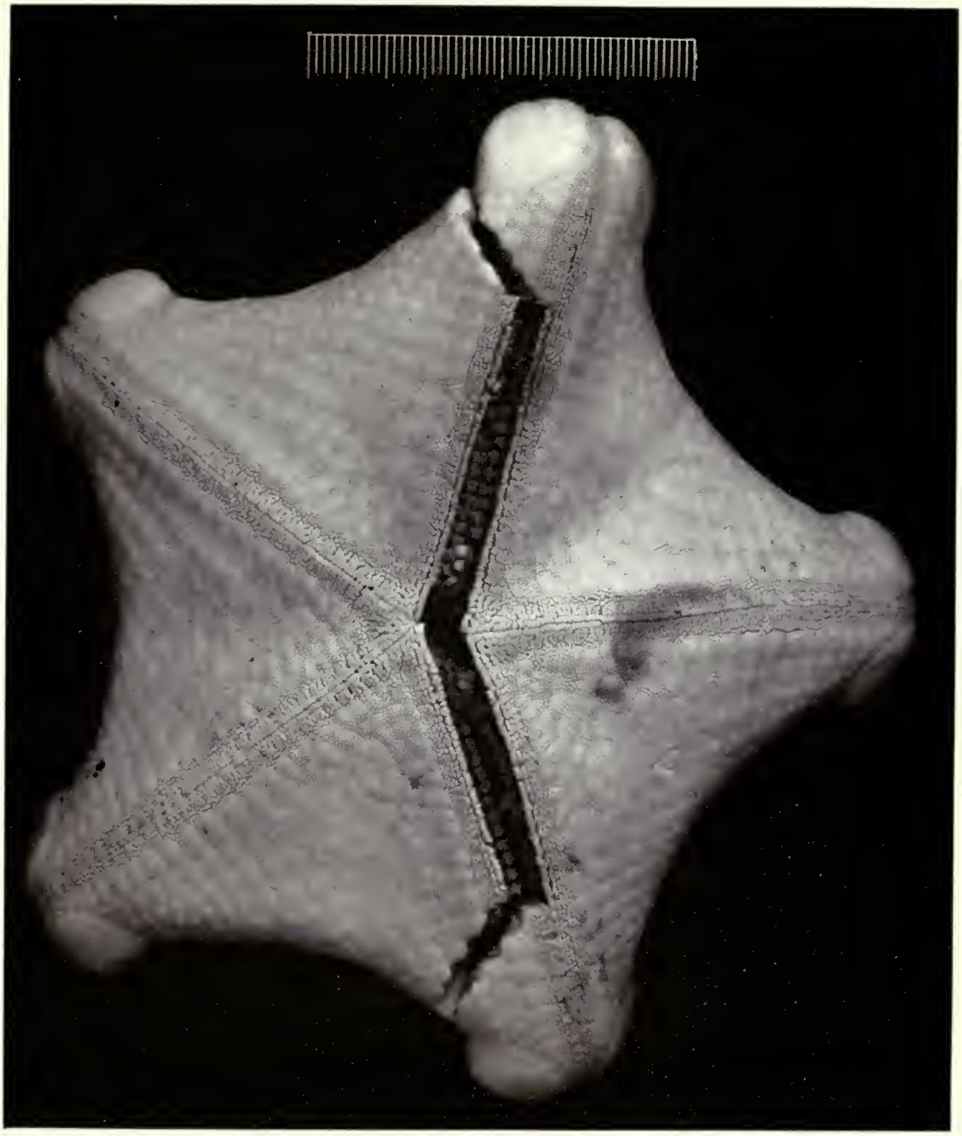


PLATE 3

FIGS 1 & 2 (right). *Spoladaster veneris* (Perrier). B.M. reg. no. 1975.12.4.164, 165. St. ST PAUL-71, dried half specimen opened out, R 58 mm, viewed internally; intact specimen, R 52 mm, viewed dorsally.

FIG. 3 (top left). *Spoladaster brachyactis* (H. L. Clark). 1904.4.20.133, False Bay, South Africa, R 58 mm, viewed dorsally.

FIG. 4 (bottom left). *Poraniomorpha hispida* (M. Sars). 91.4.15.1, Trondheim Fjord, Norway, R 40 mm, viewed dorsally. (See Pl. 4 for scale.)

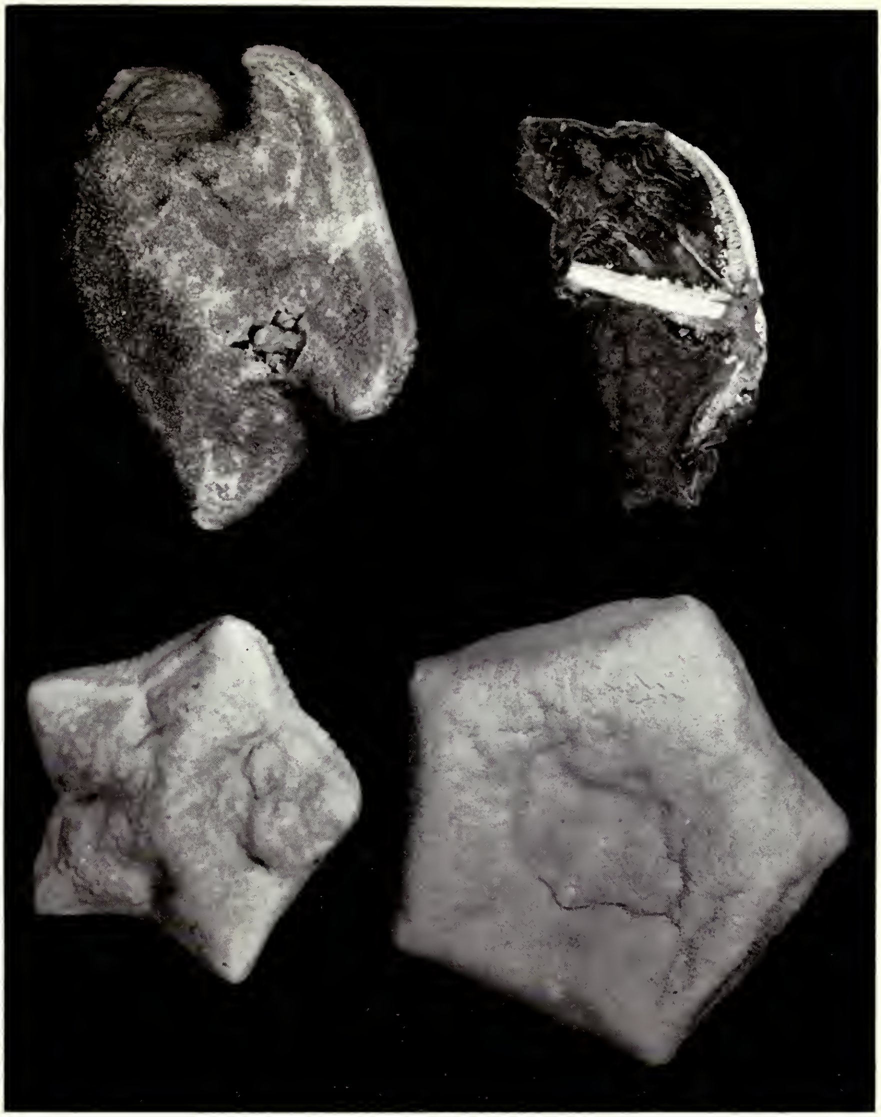


PLATE 4

Figs 1 & 2 (right). *Spoladaster veneris.*

Fig. 3 (top left). *Spoladaster brachyactis.*

Fig. 4 (bottom left). *Poraniomorpha hispida* ; all as in Pl. 3 but in external or ventral views.

Fig. 5 (centre). *Poraniomorpha hispida* forma *borealis* (Sussbach & Breckner), 1974.1.4.1, Faeroe Channel, west of Wyville Thomson Ridge, dried half specimen, side view (scale in mm).

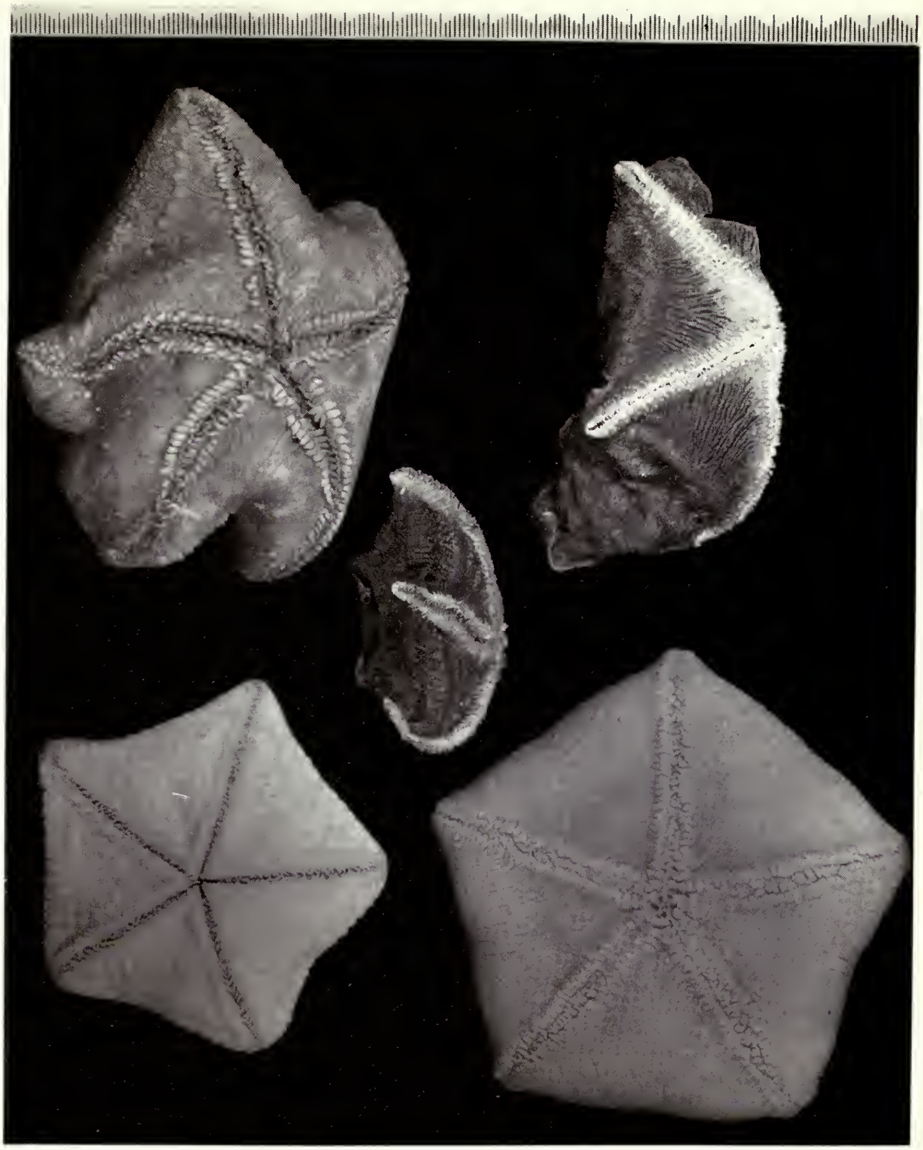


PLATE 5

Figs 1 & 2 (right). *Spoladaster veneris.*

Fig. 3 (top left). *Spoladaster brachyactis.*

Fig. 4 (bottom left). *Poraniomorpha hispida* ; all as in Pl. 3, X-radiographs.

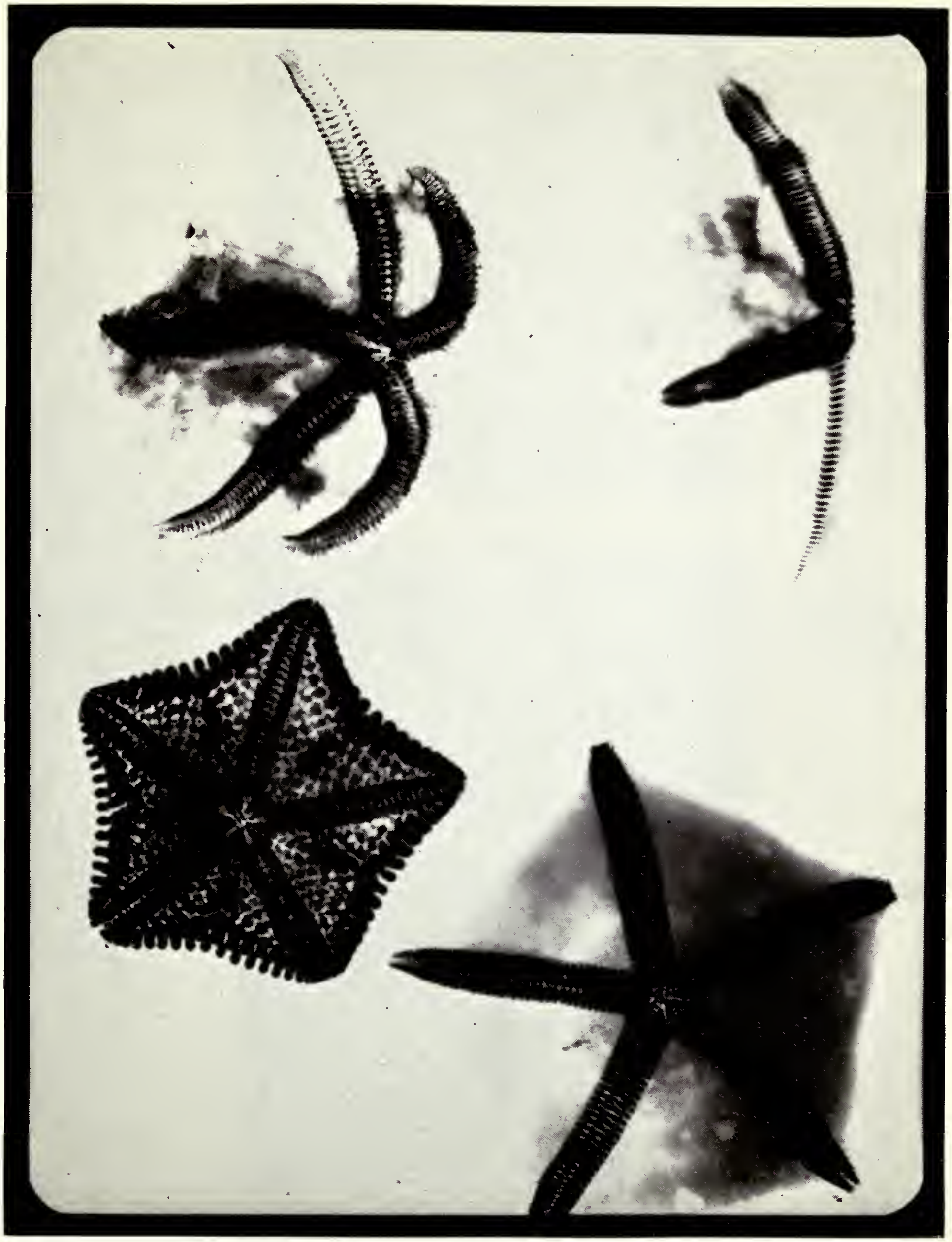
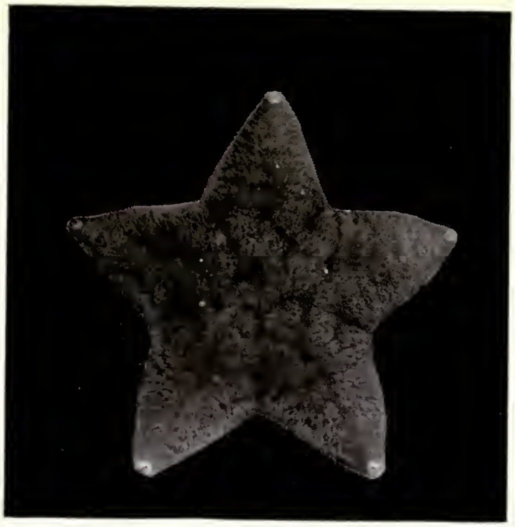
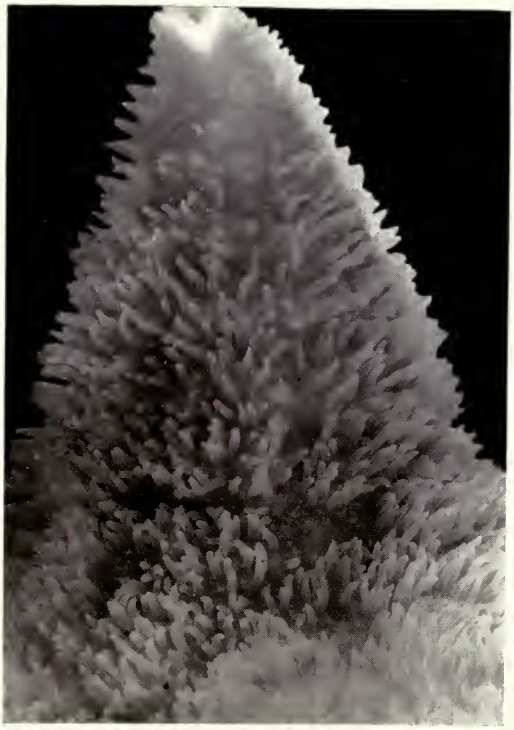


PLATE 6

Spoladaster veneris (Perrier). Live whole specimen and one ray in dorsal view, photographed by Dr Beurois. (Superimposed on black.)





RESTRICTION OF THE FAMILY PORANIIDAE, *SENSU* SPENCER & WRIGHT, 1966 (ECHINODERMATA: ASTEROIDEA)

By FREDERICK H. C. HOTCHKISS AND AILSA M. CLARK

SYNOPSIS

The amalgamation of two families of asteroids under the name Poraniidae in the Asterozoa section of the *Treatise on invertebrate paleontology* by Spencer & Wright (1966) is here rejected on the basis of the fundamentally different arrangement of the actinal plates in the two groups of genera concerned.

INTRODUCTION

THE initiative for this note and the observation on which it is based came from one of us (F. H. C. H.), the history of the problem being dealt with by the other. The specimens used to illustrate it were specially prepared (by treatment with KOH followed by glycerine to increase the transparency of the normally opaque skin and reveal the skeleton) by Mr R. H. Harris of the Histology and Preservation Section of the Zoology Department, British Museum (Natural History), and photographed to emphasize further the skeletal structure by Mr P. A. Richens of the Photographic Unit of the Museum, to whom we are indebted.

HISTORY

In 1840 three nominal genera of stellate, thick-skinned asteroids were described:

(1) *Asterope* Müller & Troschel (1840a) with type *Asterias carinifera* Lamarck, 1816, by monotypy, renamed *Asteropsis* by the same authors (1840b) several months later (without explanation but presumably because they had found the first name preoccupied);

(2) *Gymnasteria* Gray for *G. spinosa* and *G. inermis* spp. nov.; and

(3) *Porania* Gray for '*Asterias gibbosa* Leach', said to be Leach 1817 but probably from an MS catalogue of the British Museum collections. (This is not the same species as *Asterias gibbosa* Pennant, 1777, which Gray gives as *Asterina gibbosa* on the next page.) Gray's paper was published in December, 1840 and post-dated both of Müller & Troschel's (see Fisher, 1908).

In their main work, the *System der Asteriden* in 1842, Müller and Troschel cited both *Gymnasteria* and *Porania* as synonyms of *Asteropsis*. They included in the genus *A. carinifera* (Lamarck), *Asteropsis ctenacantha* sp. nov. (referred to the synonymy of *Porania pulvillus* (O. F. Müller) by Perrier, 1875), *Asterias pulvillus*

Bull. Br. Mus. nat. Hist. (Zool.) **30**, 6 *Issued* 25 *November* 1976

O. F. Müller, 1788, with synonym *Porania gibbosa* Gray, and *Asterias vernicina* Lamarck, 1816; also in a postscript Gray's *Gymnasteria spinosa* and *G. inermis*, which they thought to be conspecific at least with each other.

After study of Gray's types of *G. spinosa* and *G. inermis* in the British Museum collections, Perrier (1875 : 285) referred both to the synonymy of *Asterias carinifera* Lamarck. This should automatically have relegated *Gymnasteria* Gray where it belongs in the synonymy of *Asteropsis* Müller & Troschel. Although Perrier was aware of Müller & Troschel's usage of *Asteropsis* in 1840 before Gray's of *Gymnasteria* (see 1875 : 9–10), for some reason he retained the name *Gymnasteria* for *A. carinifera* and at the same time improperly emended *Asteropsis* to include only *Asterias vernicina* Lamarck, ineligible as type-species since not included in 1840. Since he simultaneously synonymized *Petricia punctata* Gray, 1847, the type species of *Petricia* Gray, with *A. vernicina*, this move dispensed with a valid generic name while perpetuating at the same time an invalid one.

Unfortunately Sladen was apparently unaware that Müller & Troschel had used *Asteropsis* already in 1840 and perpetuated Perrier's errors until they were pointed out by Fisher (1908 and 1911 : 247, 248) when he noted that *Asterope* Müller & Troschel, 1840 is not invalidated by *Asterope* Philippi, 1840, having been published at least two months earlier. He therefore referred *Gymnasteria* Gray to the synonymy of *Asterope*, rejected *Asteropsis* as superfluous and revived *Petricia* Gray from synonymy.

As for the family position of these genera, in 1875 Perrier included *Porania*, *Asteropsis* (emended), *Dermasterias* nov. and *Gymnasteria* at the end of the Goniasteridae, following them with the Asterinidae and implying some affinity with the latter family. In 1879 Viguier referred the first three genera to the Asterinidae. However, in 1884 Perrier divided the families of asteroids into named orders, placing the Asterinidae in the order Spinulosae but establishing a new family Gymnasteriadae in the order Valvulatae (p. 165) (although on p. 154 he lists a family Asteropsidae in the order Valvatae !). Included in the Gymnasteriadae were *Gymnasteria*, *Porania*, *Asteropsis*, *Dermasterias* and *Marginaster* gen. nov. In the *Challenger* report, Sladen (1889 : 355–356) adopted Gymnasteriidae (with corrected spelling) and added *Tylaster* and *Poraniomorpha*, both of Danielssen & Koren, 1881, also *Rhegaster* Sladen, 1883 and *Lasiaster* gen. nov.; he commented on the affinity of some of these with the Asterinidae.

After discovery of the echinasterid which he called *Poraniopsis*, Perrier in 1891 (pp. 107, 163) removed *Porania* from the Gymnasteriidae to the Asterinidae, adjacent to the Echinasteridae in the order Spinulosae. He made no mention in the discussion of *Porania* that it should be referred to a family of its own but in 1894 (p. 163) took this action, though citing 'Poraniidae Perrier, 1891'. This is more puzzling because in his preliminary discussion on classification in the 1894 *Travailleur* and *Talisman* report he makes not the slightest mention of Poraniidae and indeed lists *Marginaster pentagonus* (the only relevant species collected by these vessels) under the family Pentagonasteridae (i.e. Goniasteridae) on p. 30. On p. 163 he placed Poraniidae in the Spinulosae and included in it *Porania*, *Tylaster*, *Poraniomorpha*, *Marginaster*, *Rhegaster* and *Lasiaster*. This would leave only *Gymnasteria*, *Asteropsis* and

Dermasterias in the family Gymnasteriidae, which is listed on p. 327 under the order Valvata [sic]).

Having in 1908 renamed as Asteropidae Perrier's Gymnasteriidae, in 1911 Fisher referred *Porania* and its relatives to the Asteropidae. Verrill (1914 : 304) expressed doubt about this because of affinity of *Porania* with the Asterinidae and in 1919 Fisher separated them again, though removing also *Dermasterias* to the Poraniidae, leaving only *Asterope* and *Petricia* in the Asteropidae.

In the years following, several new nominal genera were added to the Poraniidae, while others were synonymized. Mortensen (1933 : 249) included under the heading Asteropidae *Tylaster meridionalis* and *'Cryaster' brachyactis* (both more closely related to *Porania* than to *Asterope*) ; then Fisher (1940 : 136) named a new genus *Spoladaster* for *C. brachyactis*, again giving the family as Asteropidae (while on p. 154 he deals separately with the family Poraniidae) a treatment also followed by A. M. Clark in 1952. H. L. Clark (1946 : 109) also evidently considered that Poraniidae and Asteropidae can be kept distinct. However, Madsen (1959 :153) refers to *Porania* under Asteropidae, order Spinulosa.

Spencer & Wright (1966 : U69) in the *Treatise on invertebrate paleontology* again unite the two groups of genera but under the name Poraniidae Perrier, 1894, in the order Spinulosida. They also show that *Asterope* Müller & Troschel is after all invalid, being preoccupied by *Asterope* Hübner, 1819, an insect, and must be replaced by *Asteropsis* (a fact noted independently by A. M. Clark in 1967).

TAXONOMY

Clearly with so much anomalous treatment it is time that this problem was re-examined by further study of the skeleton obscured beneath the thick skin of these asteroids. The use of X-radiography by Dons (1936, 1938) and Madsen (1959) has revealed the extent of reduction of the skeleton in some species related to *Porania* and even more to *Poraniomorpha* but it is comparison between the better-calcified *Porania* itself and *Asteropsis* that is needed.

Examination revealed that there are two fundamentally different arrangements of the plates in the triangular actinal intermediate areas under each side of the arm among the genera of Poraniidae *sensu* Spencer & Wright. In *Porania* itself and also *Poraniomorpha* and *Tylaster*, for instance, the arrangement consists of rows of actinal plates running parallel to the inferomarginals, the zone of plate addition is adjacent to the adambulacrals and the shortest row is in the proximal part of the interradial area near the oral plates (Pl. 1). Conversely, in *Asteropsis*, *Dermasterias* and *Petricia* the arrangement consists of rows of plates running parallel to the adambulacrals, the zone of addition is adjacent to the inferomarginals and the shortest row adjoins the interradial inferomarginals in the distal part of the interradial area (Pl. 2 ; Pl. 3). The second pattern is the usual one in the families of the order Valvatida (e.g. Goniasteridae and Oreasteridae) as well as in some Spinulosida (e.g. Asterinidae).

It is therefore possible to divide the genera concerned into two distinct groups. In the cases where the actinal plates are either few and irregular (e.g. the diminutive species referred to *Marginaster**) or extremely reduced (e.g. *Spoladaster* and *Tylaster*) by resorption in adults, the pattern can be estimated by the locus of plate formation, judged by the sizes of the plates or the positions of the surviving plates when the older ones have been resorbed.

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* Which I think may all prove to be based on juveniles of other Poraniid genera. A. M. C.

The two groups of genera are as follows :

PORANIIDAE Perrier, 1894
Porania Gray, 1840
Chondraster Verrill, 1895
Marginaster Perrier, 1881
Poraniella Verrill, 1914
Poraniomorpha Danielssen & Koren, 1881
Poranisca Verrill, 1914
Pseudoporania Dons, 1936
Sphaeriaster Dons, 1939
Spoladaster Fisher, 1940
Tylaster Danielssen & Koren, 1881

ASTEROPSEIDAE[*] Hotchkiss & Clark, 1976
Asteropsis Müller & Troschel, 1840
Dermasterias Perrier, 1875
Petricia Gray, 1847

The Triassic genus *Trichasteropsis* Eck, 1879 (illustrated by Spencer & Wright, 1966, fig. 43.3a–c) has poraniid actinal growth gradients and should be transferred to the Poraniidae from the Palasterinidae (order Paxillosida).

Concerning the Ordovician somasteroid *Chinianaster levyi* Thoral, Spencer's reconstruction of this (1951, fig. 7 ; Spencer & Wright, 1966, fig. 39.4) shows poraniid-

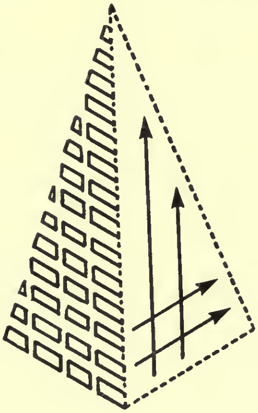

Fig. 1.

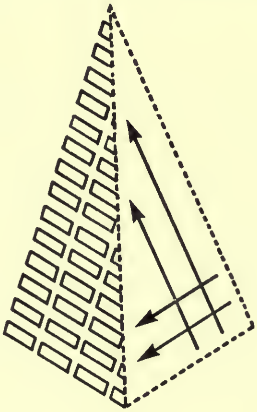

Fig. 2.

FIG. 1. Diagram showing orientation and polarity of growth gradients as observed by Fell.

FIG. 2. Diagram showing orientation and polarity of growth gradients observed in Poraniidae.

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[*] This family name is based on *Asteropsis* Müller & Troschel, 1840b, which is the earliest available name to replace *Asterope* Müller & Troschel, 1840a, and is a senior subjective synonym of *Gymnasteria* Gray, (Dec.), 1840 (see Müller & Troschel, 1842 : 65). Asteropsidae Perrier (1884:154) is not valid under Article 55 of the *Code* because he exluded the the type–species, *A. carinifera* Lamarck, from the type–genus, *Asteropsis*. Gymnasteriidae (as Gymnasteriadae) Perrier (1884:165), based on the junior synonym, though adopted by some nineteenth century authors, has not been used for nearly 70 years and may be considered to have lost all claims to validity under Article 40. The inserted 'e' in Asteropseidae derives from the genitive singular root Asteropse–. We are indebted to Dr R. V. Melville for help with this nomenclatorial problem.

like growth gradients, the shortest longitudinal series adjoining the ambulacra proximally. This contrasts with Fell's 'inferred appearance' of the same species (1963, fig. 11D), where minor differences in the sutures result in an asteropseid arrangement, conforming with his theories on the phylogeny of asteroids (Fig. 1). If Spencer is proved correct, then Fell's growth gradient argument for crinoid ancestry of the Asterozoa is seriously undermined.

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PLATE 1

Porania antarctica glabra Sladen. B.M. reg. no. 1948.3.16.408. Discovery Investigations St. 366, South Sandwich Islands (× 1).

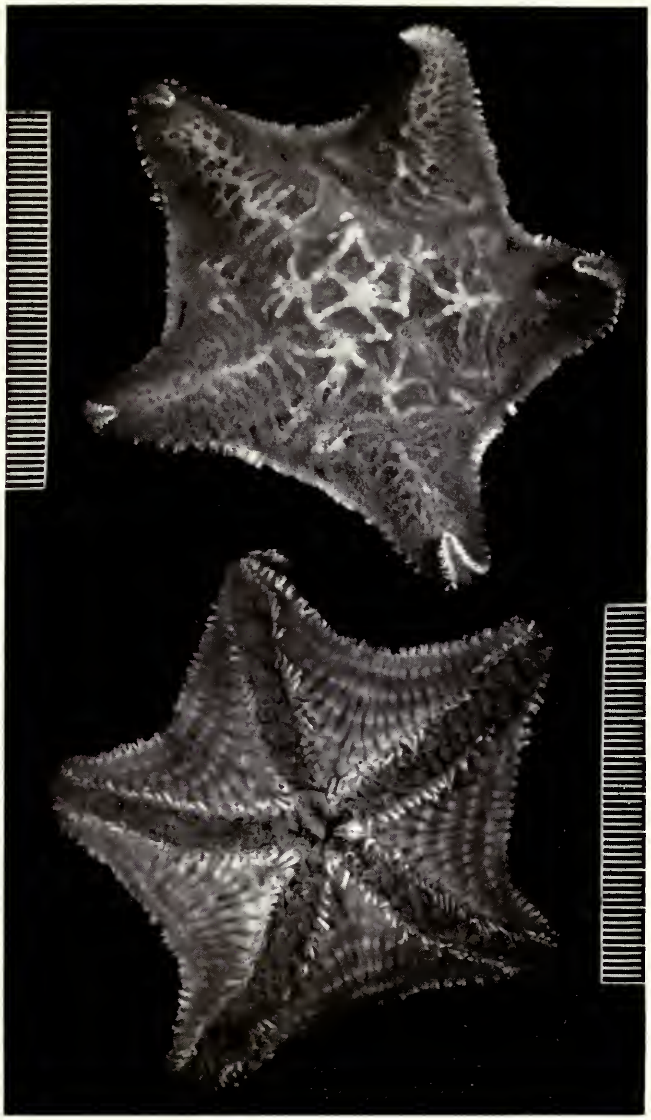


PLATE 2

Asteropsis carinifera (Lamarck). 1964.8.17.84. Red Sea (× 1).

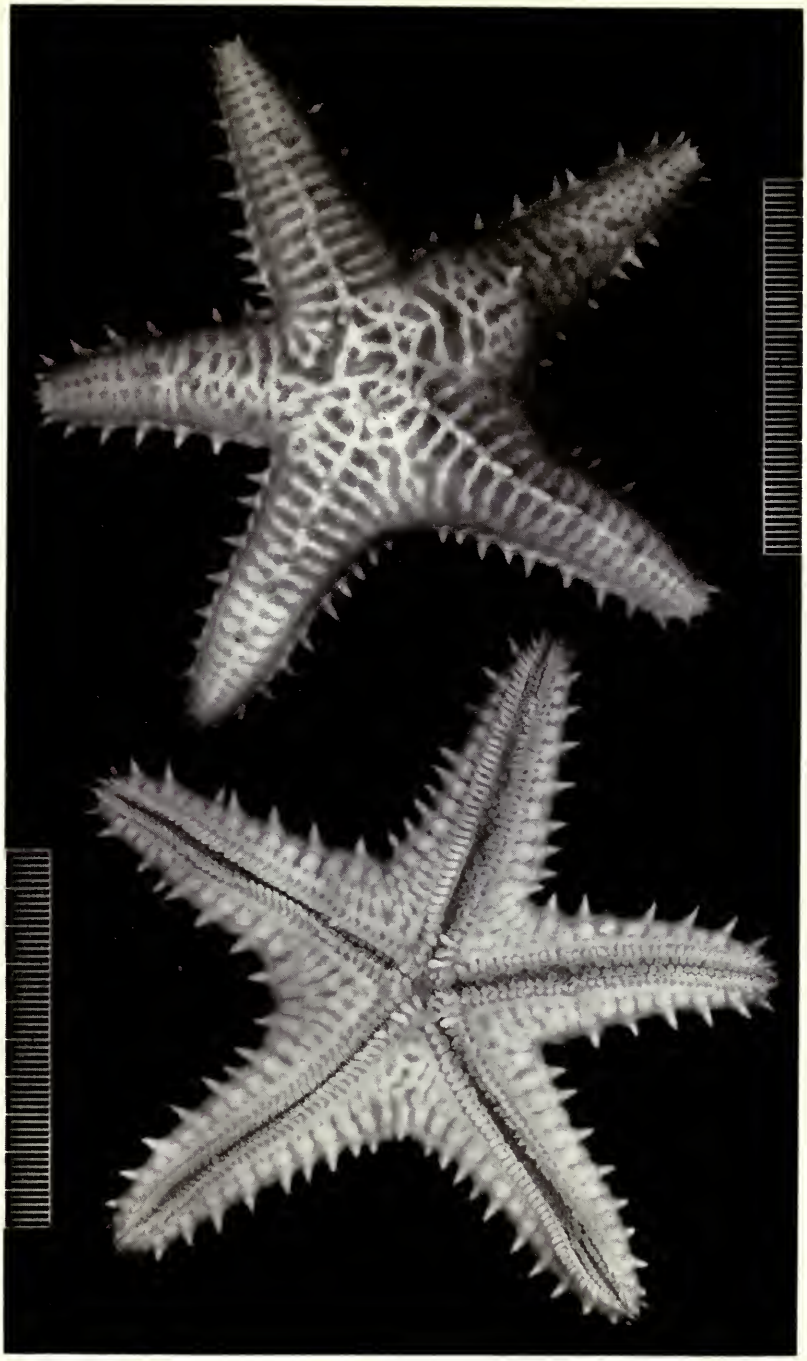
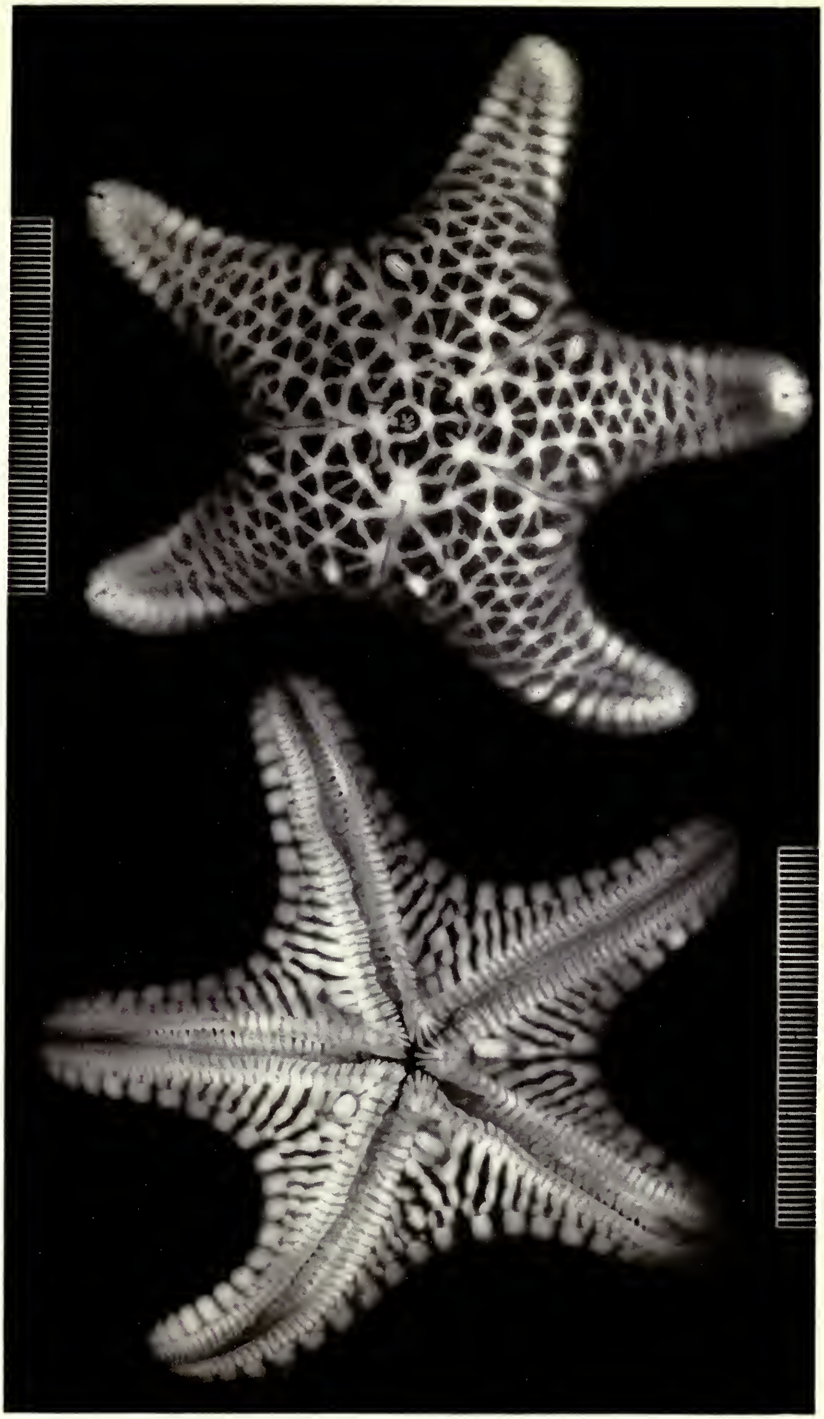


PLATE 3

Petricia vernicina (Lamarck). 1963.4.19.6. Port Noarlunga, South Australia (× 1).



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VARIATION IN EURASIAN SHREWS OF THE GENUS *CROCIDURA* (INSECTIVORA : SORICIDAE)

P. D. JENKINS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 30 No. 7
LONDON: 1976

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VARIATION IN EURASIAN SHREWS OF THE GENUS *CROCIDURA* (INSECTIVORA : SORICIDAE)

BY

PAULINA D. JENKINS

Pp 269–309 ; 14 *Text-figures*

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VARIATION IN EURASIAN SHREWS OF THE GENUS *CROCIDURA* (INSECTIVORA: SORICIDAE)

By P. D. JENKINS

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SYNOPSIS

An investigation including the use of a canonical variate analysis is made into the relationships between various species of *Crocidura* occurring in Eurasia. The status of species and their geographical variation are examined and keys are provided to aid segregation of species.

C. suaveolens is the most widespread species. *C. zarudnyi* is regarded as a distinct species showing some affinity to *C. suaveolens* and to Asian *C. russula*. *C. russula* is divisible into two main groups – Europe/Algeria and western Asia. The latter group is close to some populations of *C. suaveolens*. The European/Algerian group shows some association with western Asian *C. leucodon*. The Japanese form, *C. dsinezumi*, while somewhat similar to some populations of *C. suaveolens* and Asian *C. russula*, is sufficiently distinct to retain specific status. *C. leucodon* is also divided into European and western Asian groups and the Iranian *caspica* is considered to be a subspecies of the latter group. The affinities of the western Asian group of *C. leucodon* and *C. lasiura* are discussed. *C. fuliginosa trichura* is assigned to *C. attenuata*. *C. dracula* is allocated to *C. fuliginosa* and some of the forms recorded from Indonesia are considered to belong to this species. *C. horsfieldi* is compared with *C. suaveolens* but retained as a distinct species. Short notes are made on other species occurring in the area.

INTRODUCTION

WHITE-TOOTHED shrews of the genus *Crocidura* occur mainly southwards from latitude 53°N in the Palaearctic, Oriental and Ethiopian regions. This report is concerned with those species from the first two regions.

Ellerman & Morrison-Scott (1966) recognized only fourteen species amongst the forty four species names recorded from the Palaearctic and Indian regions. Chasen (1940) listed twenty nine species names from the Malaysian subregion of the Oriental region. It is possible that the same species occur under different names in different areas, so comparison over the entire area was considered necessary.

New forms have frequently been described from single specimens but only rarely figured and with inadequate descriptions. Information on colour of pelage, external dimensions and a few skull measurements does not seem to provide adequate diagnoses; while diagnostic characters that vary from species to species, yet are intraspecifically constant, are distinctly lacking in this genus.

This report describes geographical variation between populations occurring throughout Eurasia. A canonical variate analysis has been used to investigate relationships between populations. This type of analysis allows metrical characters of a large number of samples to be handled simultaneously but is limited to those specimens possessing all the necessary characters. The results have been correlated with all other available information and some changes to the existing taxonomy are suggested.

MATERIALS

The collections of the British Museum (Natural History) (BMNH) contain 740 specimens from Eurasia. All of these were examined and, for the sake of completeness, specimens of North African *C. russula* and *C. suaveolens* (which are mainly distributed in Europe and Asia) were included. In addition the following specimens from other institutions have been examined: Harrison Zoological Museum, Sevenoaks: *C. russula* – 28, *C. russula caspica* – 3, *C. leucodon judaica* – 2, *C. lasia* – 1; United States National Museum: *C. zarudnyi* – 9, *C. pergrisea* – 2; Naturhistorisches Museum, Vienna: *C. pergrisea arispa* – 1.

C. olivieri, *C. religiosa* and *C. floweri* from Egypt have been excluded because they are confined to Africa and are readily distinguished from Eurasian species. Since the BMNH collections do not contain any of the eight species listed by Taylor (1934) from the Philippine Islands these have also been excluded.

For the canonical variate analysis (CVA) the number of available specimens was reduced to 526, since the method demanded specimens complete for all of the characters included. In the CVA the group of specimens from each locality is referred to by the term operational taxonomic unit (OTU) followed by the number of the group (see Table 1 and Fig. 1).

TABLE 1

Populations entered in the canonical variate analysis

OTU	Locality	No. of specimens	Current species name
1	Isles of Scilly	10	*C. suaveolens cassiteridum*
2	Jersey and Sark	9	*C. suaveolens*
3	Guernsey and Alderney	15	*C. russula peta*

TABLE 1 (*Cont.*)

OTU	Locality	No. of Specimens	Current species name
4	France	11	*C. russula russula*
5	France	14	*C. leucodon leucodon*
6	Spain	7	*C. russula pulchra*
7	Portugal	8	*C. russula pulchra*
8	Algeria	16	*C. russula agilis*
9	Algeria	4	*C. suaveolens whitakeri*
10	Germany, Belgium and Holland	17	*C. russula russula*
11	Germany	9	*C. leucodon leucodon*
12	Switzerland	8	*C. suaveolens mimula*
13	Switzerland	19	*C. russula russula*
14	Switzerland	8	*C. leucodon leucodon*
15	Sicily	5	*C. sicula*
16	Sardinia	9	*C. russula ichnusae*
17	Corsica	11	*C. russula cyrnensis*
18	Rumania and Hungary	5	*C. suaveolens mimula*
19	Yugoslavia	15	*C. suaveolens mimula*
20	Yugoslavia	21	*C. leucodon*
21	Greece	8	*C. suaveolens mimula*
22	Turkey	11	*C. russula monacha*
23	Turkey	15	*C. leucodon lasia*
24	Lebanon	11	*C. russula*
25	Israel	16	*C. russula*
26	Lebanon and Israel	7	*C. leucodon judaica*
27	Iran	7	*C. russula caspica*
28	Afghanistan	5	unnamed
29	Pakistan	8	*C. zarudnyi*
30	Russian Turkestan	18	*C. suaveolens ilensis*
31	Kashmir	6	*C. russula pullata*
32	Punjab	11	unnamed
33	Sri Lanka	14	*C. horsfieldi*
34	Darjeeling	14	*C. attenuata rubricosa*
35	Bhutan	7	*C. attenuata rubricosa*
36	Assam	20	*C. attenuata rubricosa*
37	Burma	8	*C. attenuata*
38	Malaya	16	*C. malayana*
39	Borneo	7	*C. fuliginosa baluensis*
40	Christmas Island (10°31′ S, 105°33′ E)	10	*C. fuliginosa trichura*
41	Yunnan	8	*C. dracula*
42	Yunnan	4	*C. suaveolens*
43	N. Vietnam	20	*C. dracula*
44	China	9	*C. attenuata attenuata*
45	Korea	16	*C. suaveolens shantungensis*
46	Korea	15	*C. lasiura*
47	Japan	14	*C. russula dsinezumi*

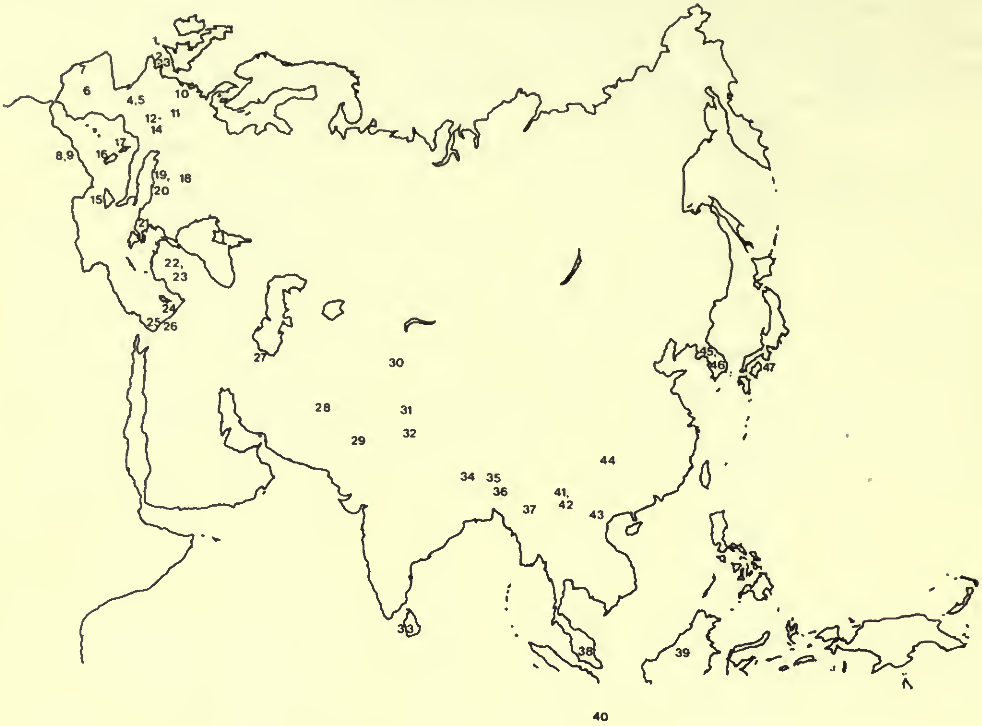

FIG. 1. Distribution map of samples entered in the canonical variate analysis.

METHODS

Characters were taken exclusively from skins and skulls because there are very few shrew skeletons in the BMNH collections, while the paucity and age of alcoholic specimens preclude the use of anatomical characters such as those of the male reproductive tract which have been used successfully by other authors (Vinogradov, 1958; Martin, 1967). The following characters were examined with the abbreviations used in the text in brackets.

Head and body length (HB)
Tail length (TL)
Hindfoot length
Ear length
Weight
Colour of pelage
Condylobasal length (CBL)
Length of upper toothrow (UTL)
Combined length of upper incisor and unicuspids
Lingual length of upper unicuspids
Labial length of upper unicuspids at cingula (LLU)
Width across maxillae at level of second molar (MB)
Height of rostrum
Lacrymal breadth
Interorbital breadth (IB)
Postglenoid breadth (PB)
Braincase breadth (BB)
Height of braincase
Length of mandible (excluding incisor)
Height of mandible at coronoid process
Length of mandibular toothrow (excluding incisor)
Shape of teeth

Skin measurements were taken from collectors' notes on the specimen labels, which are notoriously fallible because they are difficult to measure accurately and consistently and the measuring technique varies from one collector to another. However, skin measurements are still useful as long as these disadvantages are taken into account and since they have been extensively used in the taxonomy of this group their inclusion was considered necessary. The effect of using skin measurements was checked by running the CVA twice, first including head and body, tail and hindfoot length and secondly omitting these three characters. The results were found to be comparable so only the former analysis is described here.

The toothrow and anterior part of the skull are less frequently damaged than the posterior. Since the CVA requires possession of all characters by each specimen either the number of specimens or number of characters had to be reduced; the latter course was considered preferable. The excluded characters were examined and incorporated with the results of the CVA at a later stage. The following characters were selected for the CVA and found to show little correlation with each other (see Table 2):

1. Length of upper toothrow;
2. Combined length of upper incisor and unicuspids;
3. Lingual length of upper unicuspids;
4. Labial length of upper unicuspids at cingula;
5. Width across maxillae at level of second molar;
6. Head and body length;
7. Tail length;
8. Hindfoot length.

TABLE 2

Correlation matrix of characters used in the canonical variate analysis

Character	No.	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Length of upper toothrow	(1)	1·00							
Combined length of upper incisor and unicuspids	(2)	0·43	1·00						
Lingual length of upper unicuspids	(3)	0·60	0·40	1·00					
Labial length of upper unicuspids at cingula	(4)	0·55	0·38	0·60	1·00				
Width of maxillae at level of second molar	(5)	0·50	0·22	0·34	0·32	1·00			
Head and body length	(6)	0·20	0·09	0·12	0·16	0·27	1·00		
Tail length	(7)	0·35	0·08	0·28	0·27	0·24	0·32	1·00	
Hindfoot length	(8)	0·33	0·15	0·24	0·24	0·29	0·30	0·37	1·00

The CVA programs used were part of the CLASP package provided by J. C. Gower, Statistics Department, Rothamsted Experimental Station. The data, which may be thought of as a 'plot' in eight dimensions, are translated into visible form by the following treatment. The CVA program seeks a plane in this eight-dimensional space which, when the group means are projected on to the plane, best reproduces the Mahalanobis' distances between groups. The Mahalanobis' generalized distances (D^2) are akin to phenetic distances but take some account of intraspecific variation and correlation of characters (see Sneath & Sokal, 1973). If the variation between the projected group means is almost as large as the total variation in eight dimensions then the representation on the plane will be a good one. In the first analysis (a) the variation on the plane was 84% of the total and therefore the plot of group means on this plane gives a fairly accurate overall picture of the relationships between them.

The following relevant information is produced by the program: (1) Correlation matrix between characters for all specimens. (2) Distance matrix (D^2) or Mahalanobis' distances which are an index of dissimilarity between OTUs (see Table 8).

CANONICAL VARIATE ANALYSIS

(a) First analysis of all OTUs

The results of the first analysis are summarized in Fig. 2, in which OTUs are plotted on a plane which accounts for 84% of the variation, suggesting a reasonable representation of the actual relationships. Circles are calculated to include 90% of the individual specimens that combine to give the group mean, while the boundaries of currently recognized species groups are indicated by lines of differing texture (see key on figure).

OTUs Malaya (38), Borneo (39), Yunnan (41) and N. Vietnam (40) overlap but are well separated from all others and may be regarded as a distinct species, hereinafter referred to as *C. fuliginosa*. The remaining groups are disposed in a Y-shaped pattern, those at the extreme of each limb being clearly distinct.

(1) Top right – Darjeeling (34), Bhutan (35), Assam (36), China (44) correspond with *C. attenuata*, and Christmas Island specimens (40), *C. fuliginosa trichura*, are associated with this group. Burma (37) is also usually thought to belong to this species and is positioned closest to it despite showing no overlap at the 90% level.

(2) Lower centre – Isles of Scilly (1), Jersey and Sark (2), Rumania and Hungary (18), Yugoslavia (19), Greece (21), Russian Turkestan (30), Yunnan (42) and Korea (45) correspond with the classic concept of *C. suaveolens*. Showing overlap with this group is Pakistan (29) currently regarded as a distinct species, *C. zarudnyi*. Sri Lanka (33), *C. horsfieldi*, lies close to this group but does not overlap with it. *C. dsinezumi* from Japan (47) overlaps with *C. suaveolens*, *C. russula* and *C. zarudnyi*.

(3) The remainder form a central group extending to the top left which corresponds with the *russula–leucodon* complex, with *leucodon* falling at the extreme left. Those in the upper portion of this group include specimens from Turkey (23) and also Israel and Lebanon (26) and Iran (27) whose affinities are doubtful. The Korean OTU (46), *C. lasiura*, overlaps with the group at the extreme upper left.

(b) Second analysis of 42 OTUs (5 omitted)

The analysis was repeated but five OTUs were omitted to improve resolution (see Fig. 3). Those excluded were Malaya (38), Borneo (39), Yunnan (41) and

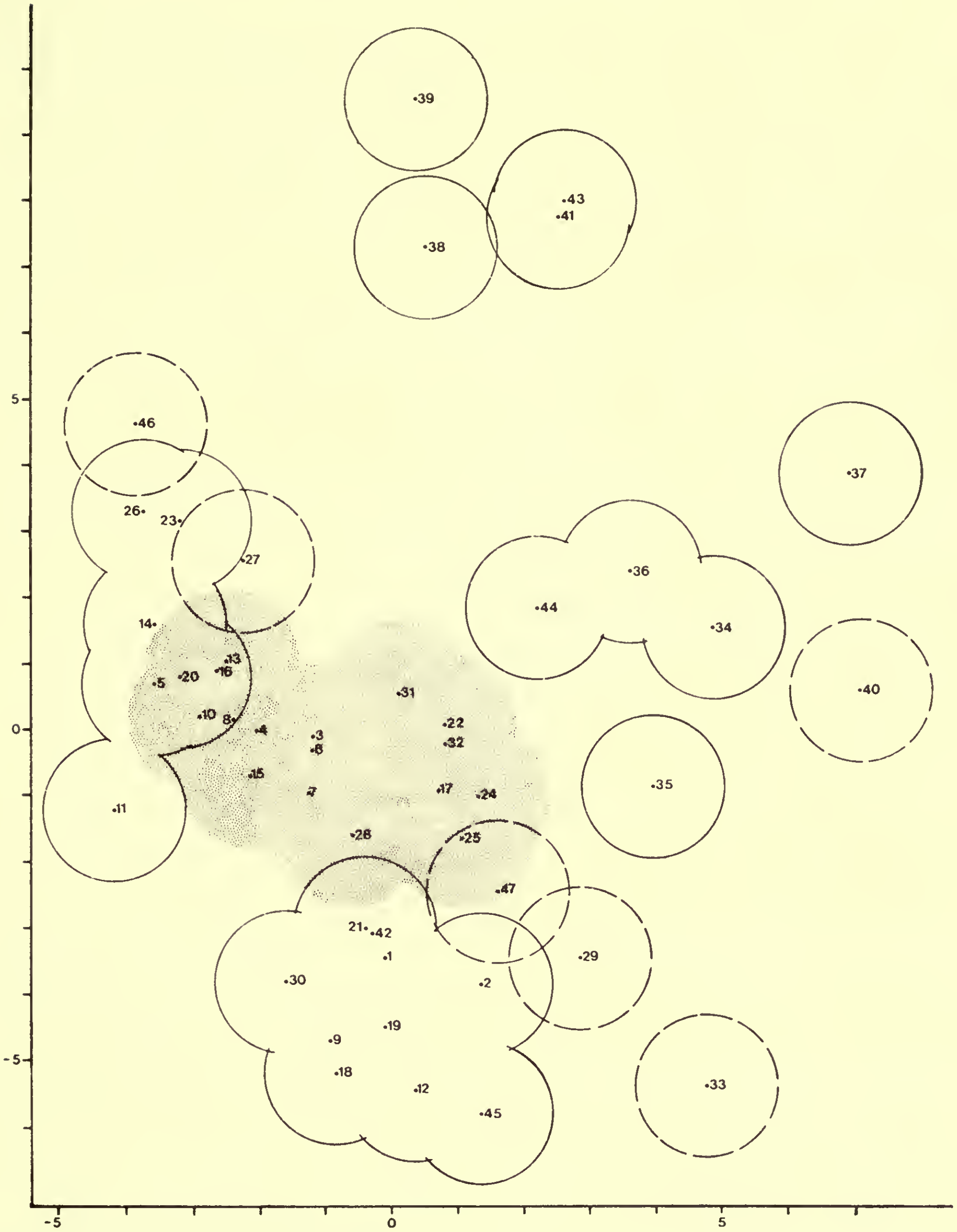

FIG. 2. First analysis of all OTUs.
C. fuliginosa – upper centre of figure ; *C. russula* – central group (stippled) ; *C. leucodon* – extreme left of central group ; *C. attenuata* – extreme right of central group ; *C. suaveolens* – lower centre of central group ; other species currently regarded as distinct – broken circles.

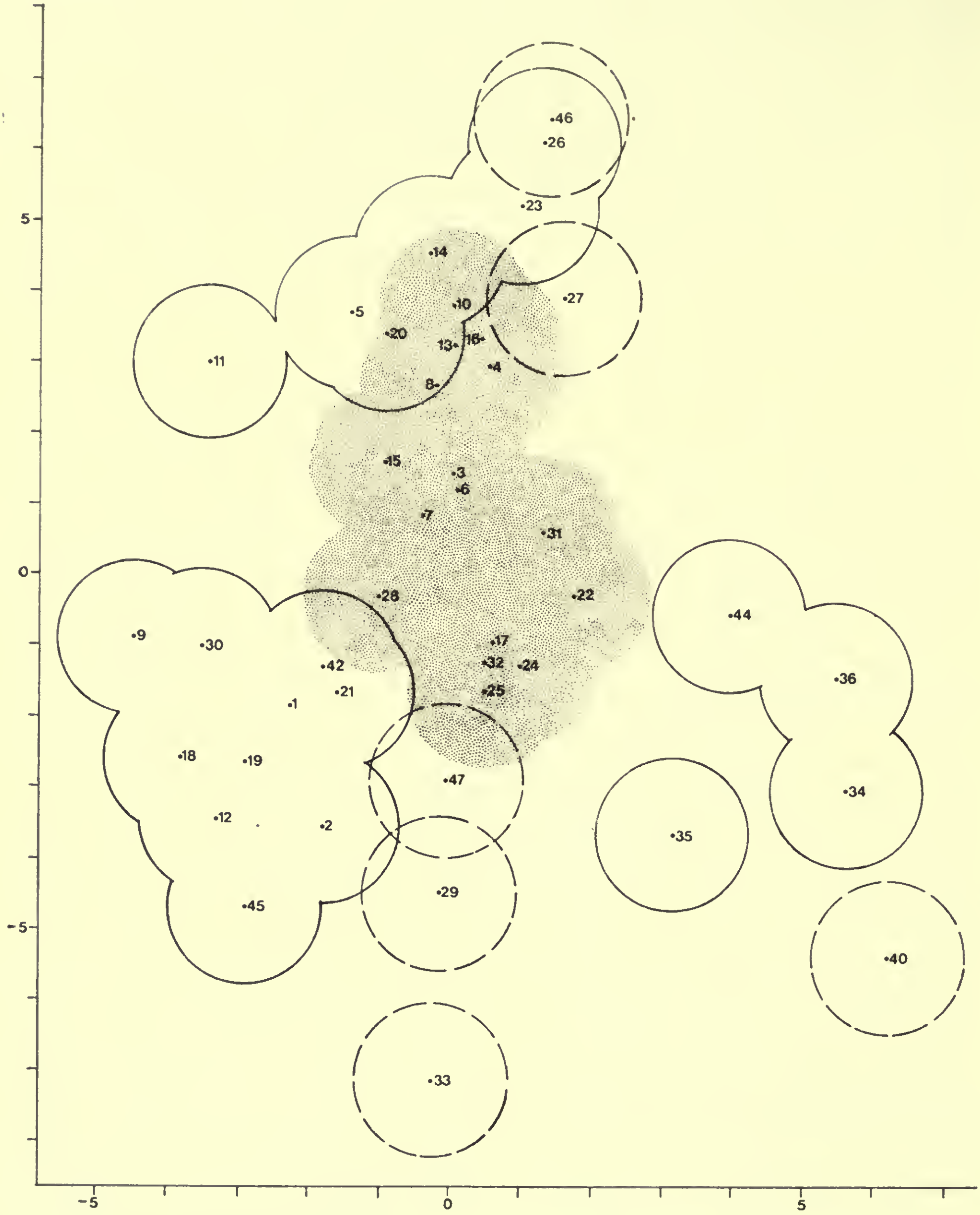

FIG. 3. Second analysis of 42 OTUs.
C. russula – central group (stippled) ; *C. leucodon* – upper left of central group ; *C. attenuata* – lower right of central group ; *C. suaveolens* – lower left of central group ; other species currently regarded as distinct – broken circles.

N. Vietnam (42) which form a distinct group, *C. fuliginosa*, and also Burma (37) which is separated from any other OTU.

The plane in this analysis includes 82% of the variation. The species groups still overlap but to a lesser extent.

(1) Lower right – OTUs Darjeeling (34), Bhutan (35), Assam (36), China (44) form the loosely knit *C. attenuata*, with which Christmas Island (40) is associated.

(2) Lower left – OTUs overlapping in the *suaveolens* group remain as before. *C. zarudnyi* overlaps with this group and *C. dsinezumi* overlaps with both groups and also with *C. russula*.

(3) The *russula–leucodon* complex is better spaced in this figure. *C. russula* falls roughly into two subgroups with most European OTUs in the upper part of the figure and Asian ones occurring lower down. *C. leucodon* lies at the top left.

IDENTIFICATION

All available information including that from the previous section is assembled here and correlated with the existing taxonomic groupings. The species recognized are :

Crocidura fuliginosa – including *malayana, baluensis* and *dracula.*
Crocidura horsfieldi
Crocidura suaveolens
Crocidura zarudnyi
Crocidura russula – two groups
Crocidura dsinezumi
Crocidura attenuata – including *C. fuliginosa trichura*
Crocidura leucodon – two groups
Crocidura lasiura

In any one locality where two or more species occur they are usually easy to separate. An exception to this is found in Switzerland where three species occur. *C. suaveolens* is readily distinguished but *C. russula* and *C. leucodon* are only clearly separable on the basis of pelage colour.

In the majority of species some populations show overlap with at least one other species and therefore an exclusive diagnosis covering the entire region is impossible. Even when the range of the genus is divided into 'European', 'eastern Asian' and an intermediate zone from Turkey east to Sri Lanka, the construction of keys presents considerable difficulties. For example, the separation of *fuliginosa* from other species of *Crocidura* depends mainly on skull length. Although the key is somewhat unsatisfactory because of the overlap in size, the degree of separation is adequate in most cases, as may be seen in Fig. 4. A similar situation obtains in other examples of overlap.

Thus while the three keys given below are not a completely accurate identification guide, they may be used to discriminate with a reasonable degree of confidence between the species from a region, particularly when a series of specimens is available.

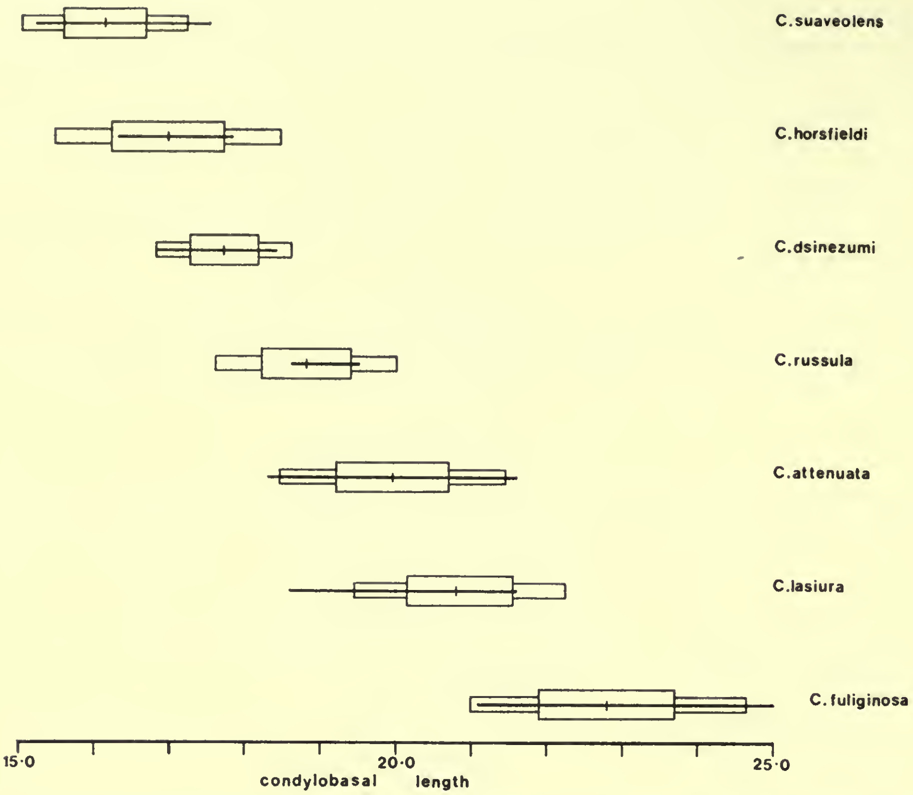

FIG. 4. Condylobasal length in species of *Crocidura* from eastern Asia, showing mean (vertical bar), range (horizontal line), one and two standard deviations (rectangles).

Confirmation of identification should be sought by reference to the additional data provided in the text.

1. KEY TO THE EUROPEAN SPECIES OF *CROCIDURA*

1 Bicoloured, pale ventral surface sharply differentiated from dark dorsum along flanks . . . . **C. leucodon**

– No sharp differentiation between dorsal and ventral colour 2

2 Average smaller, labial length of upper unicuspids up to 2·0 mm . . **C. suaveolens**

– Average larger, labial length of upper unicuspids usually over 2·0 mm . **C. russula**

Note. (a) Where *C. suaveolens* and *russula* are sympatric, they may be distinguished on the basis of size and usually by differences in the shape of the large upper premolar.

(b) *C. russula* from Corsica may be distinguished from those from elsewhere in Europe by the distinctive shape of the large upper premolar (see text and Fig. 5), and from *C. suaveolens* only by a combination of several characters. However, *C. suaveolens* is not recorded from Corsica.

2. KEY TO THE SPECIES OF *CROCIDURA* OCCURRING FROM TURKEY IN THE WEST TO SRI LANKA IN THE EAST

1 Bicoloured, pale ventral colour differentiated from dark dorsal colour along flanks or, when unicoloured, size large (upper toothrow over 8·8 mm, width across maxillae at M^2 over 6·0 mm) . . . . **C. leucodon**

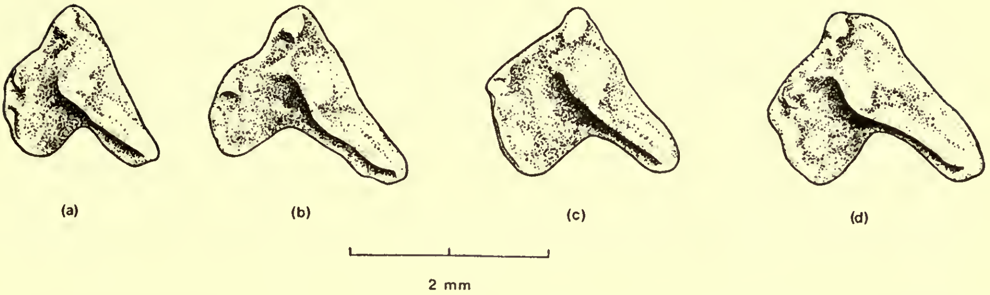

FIG. 5. Large upper premolar of European species of *Crocidura*. (a) *C. suaveolens* – Austria ; (b) *C. russula* – Corsica ; (c) *C. russula* – France ; (d) *C. leucodon* – France.

– No sharp differentiation between dorsal and ventral colour ; smaller (upper toothrow length less than 8·8 mm, width across maxillae at M^2 less than 6·0 mm . . 2

2 Lingual region of large upper premolar relatively narrow and lobed (see Fig. 6) ; labial length of upper unicuspids greater than 1·8 mm . . . ***C. russula***

– Premolar not so shaped, labial length of upper unicuspids less than 1·9 mm . . 3

3 Sri Lanka. Skull small and narrow, width across maxillae at M^2 less than 5·1 mm. Ratio of tail length to upper toothrow length 6·5–7·5 : 1 . . . ***C. horsfieldi***

– Other localities. Width of maxillae at M^2 greater than 5·0 mm. Ratio of tail length to upper toothrow length 3·4–5·2 : 1 (*suaveolens*) or if greater (4·8–7·1 : 1) colour of pelage very pale (*zarudnyi*) . . . . ***C. suaveolens***
C. zarudnyi

Note. (a) The separation of *C. russula* and the unicoloured *C. leucodon caspica* from Iran is not complete as there is a small overlap in size of the characters used. However, most specimens seen can be identified by the key above.

(b) *C. suaveolens* and *C. zarudnyi* are difficult to distinguish, see discussion in text under *C. zarudnyi*.

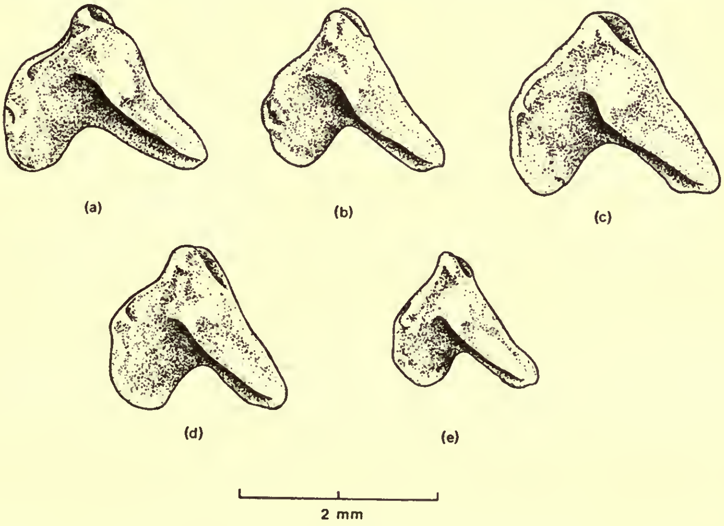

FIG. 6. Large upper premolar of species of *Crocidura* occurring from Turkey in the west to Sri Lanka in the east. (a) *C. suaveolens* – Russian Turkestan ; (b) *C. russula* – Turkey ; (c) *C. leucodon* – Turkey ; (d) *C. zarudnyi* – Pakistan ; (e) *C. horsfieldi* – Sri Lanka.

3. KEY TO EASTERN ASIAN SPECIES OF *CROCIDURA*

1	Large, condylobasal length over 21·0 mm	***C. fuliginosa***
–	Smaller, condylobasal length less than 21·6 mm, where greater than 21·0 mm, tail 48–58% of head and body length (*lasiura*) or 59–92% (*fuliginosa*). Only one specimen of *attenuata* has a condylobasal length greater than 21·0 mm – see Fig. 4 and text	2
2	Upper toothrow length 9·0–10·2 mm, tail length 34–49 mm, 48–58% of head and body length, ear margins densely furred	***C. lasiura***
–	Upper toothrow length 7·8–9·8 mm, tail length 50–88 mm, 69–108% of head and body length, ear margins not densely furred	***C. attenuata***
–	Upper toothrow length 7·4–8·8 mm, tail length 37–51 mm, 54–76% of head and body length, ear margins not densely furred	3
3	Width of braincase over 8·8 mm	***C. russula***
–	Width of braincase usually less than 8·8 mm	4
4	Japanese, width of braincase 8·1–8·8 mm, condylobasal length over 16·8 mm	***C. dsinezumi***
–	Elsewhere, width of braincase less than 8·5 mm (if from Tsushima Islands or Korea, width of braincase less than 8·2 mm and condylobasal length less than 16·9 mm)	5
5	Ratio of tail length to upper toothrow length less than 5·8 : 1	***C. suaveolens***
–	Ratio of tail length to upper toothrow length over 5·7 : 1	***C. horsfieldi***

Note. (a) Separation of *C. russula* from *C. attenuata* depends on a combination of characters, see text. (b) It is possible to distinguish *C. dsinezumi* from *C. suaveolens* occurring in nearby areas, see text. *C. dsinezumi* is geographically separated from *C. russula* and *C. horsfieldi* and a combination of characters serve to distinguish these species.

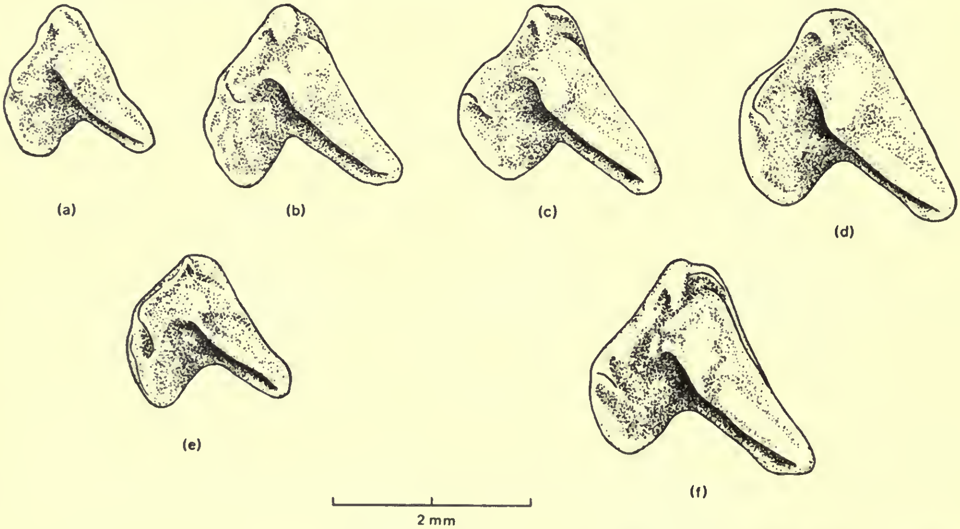

FIG. 7. Large upper premolar of *Crocidura* from eastern Asia. (a) *C. suaveolens* – Korea; (b) *C. russula* – Punjab; (c) *C. attenuata* – Assam; (d) *C. lasiura* – Korea; (e) *C. dsinezumi* – Japan; (f) *C. fuliginosa* – N. Vietnam.

VARIATION AND SYSTEMATICS

Crocidura fuliginosa (Blyth, 1855)

This is the only group that is completely distinct from all others. It includes three forms previously regarded as separate species but here associated with *C.*

fuliginosa from Burma. These are *C. malayana* from Malaya (38), *C. baluensis* from Borneo (39) and *C. dracula* from Yunnan (41) and N. Vietnam (43).

Populations from Yunnan and N. Vietnam are very similar to each other and are currently known as *C. dracula*. They have a D^2 value of 1·5 which is very low and reflects their conspecificity. These populations resemble specimens from Borneo and Malaya which, with a D^2 value between them of 2·69, are also very similar. The range of D^2 values within the group goes up to 4·3 but this is still fairly low when the geographical distance between populations and ecological barriers are taken into consideration, see distribution map (Fig. 8).

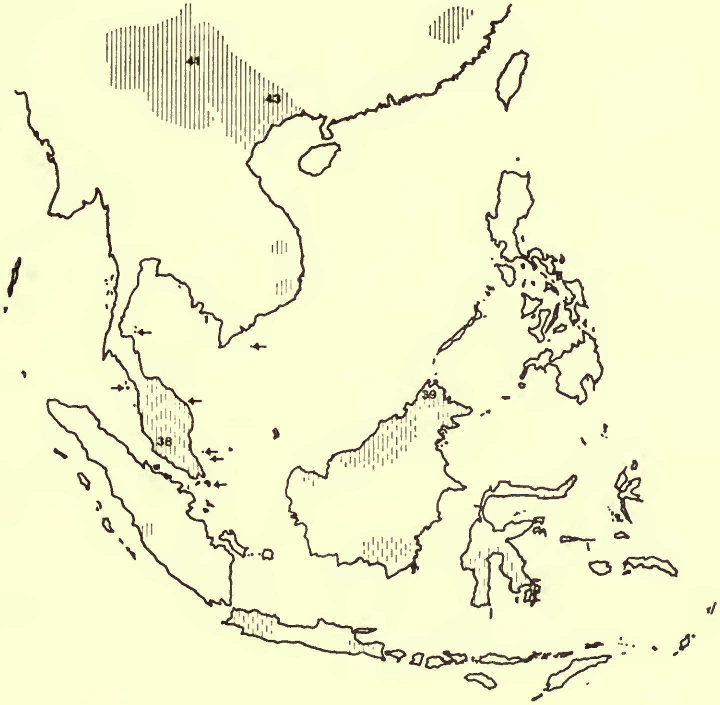

FIG. 8. Distribution of *C. fuliginosa*. Broken lines – exact distribution uncertain.

The results of the CVA may be correlated with characters not employed in the numerical analysis. This group contains some of the largest specimens in the genus. Those from Borneo are the largest while the greatest size range occurs in Malaya. Populations from Yunnan and N. Vietnam, are more similar in appearance and size to each other than to populations from Malaya or Borneo. Size range is given in Table 6.

A large number of distinct species have been described from many of the separate islands off the Malay Peninsula. The BMNH houses most of the holotypes of these, which have been compared with mainland specimens and those from Borneo. The holotypes fall within the range of this group. Some of these island forms may not even be distinct subspecies but no definite conclusions can be based on the few specimens available.

Unfortunately I have not seen the holotype of *C. fuliginosa* which was collected from Schwe Gyen, Pegu, Burma, and is lodged in the Calcutta Museum. Banks (1931) recorded it as the commonest lowland shrew in Borneo and Chasen (1940) accepted a brown form in the lowlands of Malaya as *fuliginosa* and a darker form as *malayana*.

The name *C. fuliginosa* is the subject of some confusion. Blyth's (1855) original description is rather scanty and there is some doubt whether the subsequent description by Anderson (1881) refers to the same specimen, especially as different terminology is used for measurements. The statement by Lindsay (1929) '. . . . the specific name of *fuliginosus* which Blyth plainly applied to a *Suncus*' is erroneous since *Suncus* is defined as possessing four upper unicuspids. Medway (1965) has attempted to elucidate the situation but there is still some doubt about the identity of the holotype, particularly as some label mixing may have occurred in the past.

This report confirms the view of Medway (1965) who allocated Malayan specimens of *malayana* and Bornean *foetida*, *kelabit* and *baluensis* to *C. fuliginosa*. This name is also applicable to the large specimens from the offshore islands of Malaysia as well as to specimens of *dracula* from Yunnan and N. Vietnam.

C. fuliginosa is recorded from S. Vietnam by Van Peenan, Ryan & Light (1969) which suggests a fairly continuous distribution from Yunnan in the north, lower Burma, N. and S. Vietnam to the Malay Peninsula and Borneo (see Fig. 8). A limited number of specimens indicate that this species is also present on the islands of Sumatra, Java and Sulawesi.

The following subspecific groups are suggested in addition to *C. f. fuliginosa* from Burma :

Crocidura fuliginosa malayana Robinson and Kloss, 1911. Mainland of Malaya.

Probable synonyms of *C. f. malayana* from the offshore islands of the Malay Peninsula are :

Crocidura aoris Robinson, 1912. Aor Island.
Crocidura klossii Robinson, 1912. Great Redang Island.
Crocidura negligens Robinson & Kloss, 1914. Samui Island.
Crocidura maporensis Robinson & Kloss, 1916. Mapor Island.
Crocidura gravida Kloss, 1917. Dayang Bunting Island.
Crocidura tionis Kloss, 1917. Tioman Island.
Crocidura aagaardi Kloss, 1917. Bang Nara, Patani, southern Thailand.

Crocidura fuliginosa baluensis Thomas, 1898. Borneo.

Probable synonyms are :

Crocidura foetida Peters, 1870. Borneo. This name would predate *C. f. baluensis* as the correct subspecific name.
Crocidura fuliginosa kelabit Medway, 1963. Bario, Baram District, Sarawak.

Crocidura fuliginosa dracula Thomas, 1912. Yunnan.

Crocidura praedax Thomas, 1923. Likiang Valley, Central Yunnan.

Crocidura grisescens Howell, 1928. Kuatun, Fokien, South-eastern China (listed as a synonym of *C. dracula* by Ellerman & Morrison-Scott, 1966).

Crocidura dracula mansumensis Carter, 1942. Mansum, northern Burma.

Other species occurring in the same area as *C. fuliginosa*, but readily distinguished by their small size, are *C. suaveolens* in Yunnan and N. Vietnam (condylobasal length 15·2–17·5 mm) and *C. monticola* in Borneo (condylobasal length of one specimen only 15·2 mm). Condylobasal length of *C. fuliginosa* is over 21.0 mm. *C. attenuata* is also sympatric at least in the northern part of the range but is usually distinguishable on the basis of small size. While there are no members of both species from the same area in the BMNH collections, specimens from relatively close areas, such as *fuliginosa* from Yunnan and N. Vietnam and Chinese *attenuata*, are distinct. Overlap in size occurs in some large specimens of *attenuata* from Assam and Burma and a few small *fuliginosa* from Malaya.

Crocidura horsfieldi (Tomes, 1856)

Only one OTU of this species, Sri Lanka (33), was entered in the CVA. It is rather similar to *C. suaveolens* but can be distinguished by the following features : the skull is relatively short and narrow and in these proportions it is most similar to populations of *C. suaveolens* from Tsushima Island (Japan), N. Vietnam and Korea but considerably smaller than the remaining populations (see Table 3). The tail is proportionately much longer than in *C. suaveolens*, the ratio of tail length to upper toothrow length ranging from 3·4 to 6·1 : 1 in the latter and from 6·5 to 7·5 : 1 in *C. horsfieldi*. The upper premolar is small and comparatively narrow (see Fig. 6).

The distribution of the nominate form and the other subspecies of *C. horsfieldi* listed by Ellerman & Morrison-Scott (1966) is given in Fig. 9. Of these the holotype of *C. h. indochinensis*, in the BMNH collections, agrees very well with specimens of *C. horsfieldi* from Sri Lanka and there seems little doubt that it is correctly assigned to this species. There is also a single specimen of *C. watasei* and this too is very similar to Sri Lanka specimens ; Imaizumi (1970) gives the Japanese distribution of this subspecies. Two skulls from Taiwan are larger than Sri Lanka specimens (see Table 3). Another subspecies, *C. h. wuchihensis*, described from Hainan, differs slightly from specimens from Sri Lanka (condylobasal length 15·5–15·7 mm, skull width 7·8 mm, tail 67% of head and body length).

The subspecies recorded are :

C. h. horsfieldi (Tomes, 1856). Sri Lanka.

C. h. indochinensis Robinson and Kloss, 1922. Dalat, S. Annam.

C. h. watasei Kuroda, 1924. Liukiu Islands.

C. h. tadae Tokuda and Kano, 1936. Kôtô-shô, island E. of Taiwan.

C. h. wuchihensis Wang, 1966. Mt Wuchih, Hainan Island.

The only other species recorded from Sri Lanka is *C. miya* Phillips, 1929 which is a much larger shrew, condylobasal length of holotype 19·7 mm, upper toothrow length 8·7 mm, braincase damaged but width across maxilla at second molar 5·9 mm (see p. 302).

TABLE 3

Size range of *C. horsfieldi*, *C. suaveolens*, *C. russula*, *C. zarudnyi* and *C. dsinezumi*

	Condylobasal length, mm	Upper toothrow length, mm	Width of maxillae at M^2, mm	Braincase breadth, mm
C. horsfieldi Sri Lanka	16·2–17·2	6·8–7·4	4·8–5·1	7·4–7·8
	x̄ 16·60	x̄ 7·05	x̄ 5·00	x̄ 7·60
Taiwan	17·8	7·5 and 8·0	5·5	8·5
C. suaveolens Korea,	15·2–16·9	6·7–7·7	4·7–5·3	7·0–8·2
Tsushima, N. Vietnam	x̄ 16·03	x̄ 7·17	x̄ 4·98	x̄ 7·74
Europe, Algeria, Russian	15·7–18·1	6·9–8·4	4·8–5·8	7·7–8·8
Turkestan, Yunnan	x̄ 16·89	x̄ 7·59	x̄ 5·28	x̄ 8·1
C. russula Asia	17·5–19·5	7·6–8·8	5·2–6·0	8·4–9·4
	x̄ 18·39	x̄ 8·28	x̄ 5·65	x̄ 8·91
Europe	17·5–20·1	7·6–9·2	5·4–6·5	8·5–9·5
	x̄ 18·79	x̄ 8·48	x̄ 5·89	x̄ 8·97
C. zarudnyi Pakistan,	16·1–18·8	7·1–8·3	5·0–5·5	7·8–8·5
Punjab, Turkey, Iran	x̄ 17·69	x̄ 7·78	x̄ 5·30	x̄ 8·25
C. dsinezumi Japan	16·8–18·4	7·4–8·1	5·1–5·9	8·1–8·9
	x̄ 16·03	x̄ 7·82	x̄ 5·50	x̄ 8·53

Crocidura suaveolens (Pallas, 1811)

The following OTUs are included in this species: Isles of Scilly (1), Jersey and Sark (2), Algeria (9), Switzerland (12), Rumania and Hungary (18), Yugoslavia (19), Greece (21), Russian Turkestan (30), Yunnan (42) and Korea (45).

The *suaveolens* group has a very large distributional range but geographical variation is not very pronounced and most Mahalanobis' distances are correspondingly low, varying from 2 to 3. The European group of Switzerland (12), Rumania and Hungary (18), Yugoslavia (19) and Greece (21) have low D^2 values of 2·03–2·87.

The Algerian, Russian Turkestan and Yunnan populations are similar in size to European ones; the remaining Asian populations from Korea, Tsushima (Japan) and N. Vietnam are on average smaller, see Table 3.

In this species there is rather more colour variation than in most of the others. Most are greyish-brown often with a slightly paler venter but certain populations, notably those occurring in arid habitats such as Russian Turkestan, Algeria and Israel, have a strikingly pale grey or fawn dorsum and a still paler venter.

Another character which is probably ecologically linked is the densely furred ear margins which distinguish Korean specimens (though nearby specimens from Tsushima, Japan, lack this character) and also specimens from Russian Turkestan, especially those from Semiretchensk. In Korea this character may be subject to a certain amount of seasonal variation; the ears of specimens in summer pelage in

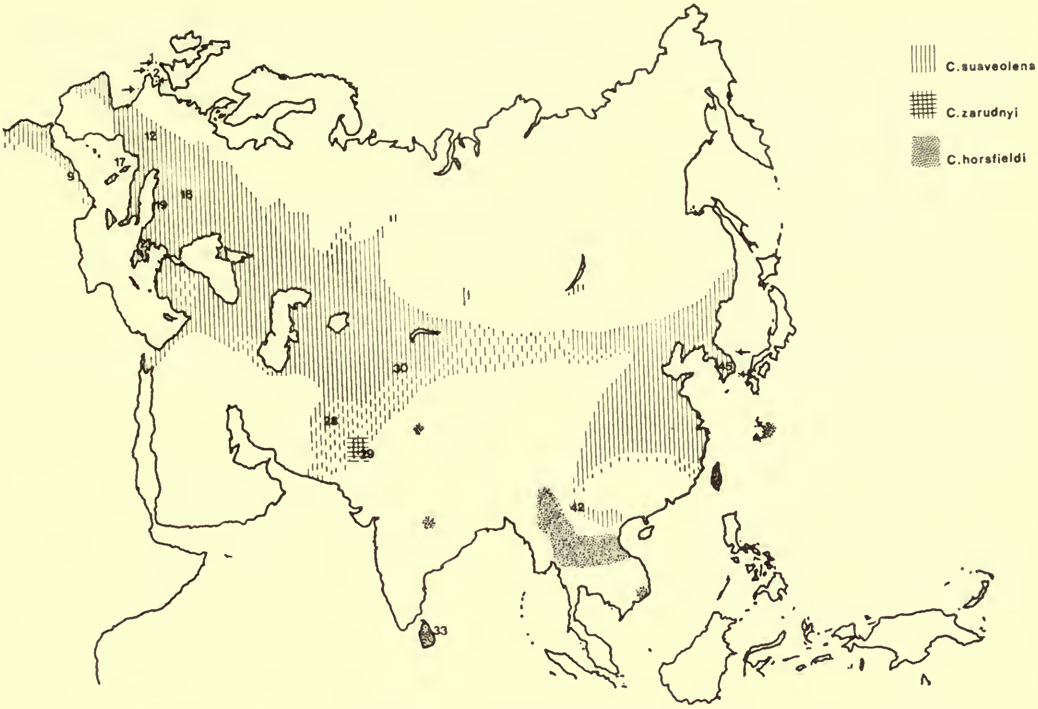

FIG. 9. Distribution of *C. suaveolens*, *C. zarudnyi* and *C. horsfieldi*. Broken lines – exact distribution uncertain.

August, September and early October are only slightly haired, while by late November, December and January specimens have winter pelage and densely furred ears.

Geographical proximity does not always correspond with low values of D^2, especially where ecological barriers are involved. For example, island populations such as the Isles of Scilly (1) and Jersey and Sark (2) are relatively close to each other but the D^2 value is 3·15. Specimens from the Isles of Scilly are most similar to those from Yugoslavia (19), with a D^2 value of 1·96, while those from Jersey and Sark are most similar to Pakistan (29) specimens of *C. zarudnyi* with a D^2 value of 2·94. Delany & Healy (1966), in their study of *Crocidura* of the Channel Islands and the Isles of Scilly, also found that populations from Jersey and Sark can be distinguished from each other and that Channel Island populations are very distinct from those from the Isles of Scilly.

In summary, European mainland populations are generally more homogeneous than the island populations, the Algerian or the Asian populations which are sampled from well-separated areas. However, despite this geographical variation there is little doubt that the populations are truly representatives of one very widespread species probably with an almost continuous distribution over its range (see Fig. 9).

Of the subspecies listed from the Palaearctic and Indian region by Ellerman & Morrison-Scott (1966), the U.S.S.R. by Gureev (1971), China by Allen (1938) (listed under *C. ilensis*) and Japan by Imaizumi (1970), the following have been examined :

C. s. mimula Miller, 1901b. Western Europe (12, 18, 19, 21).
C. s. cassiteridum Hinton, 1924. Isles of Scilly (1).
C. s. whitakeri de Winton, 1897. Morocco, Algeria (9).
C. s. ilensis Miller, 1901c. Russian Turkestan to Mongolia (30).
C. s. shantungensis Miller, 1901c. Korea, Tsushima Islands (Japan), China (45).

Also samples from Jersey and Sark (2) and Yunnan (42).

Mahalanobis' distances between some populations of *C. suaveolens* (Isles of Scilly (1), Yugoslavia (19), Greece (21), Russian Turkestan (30) and Yunnan (42))

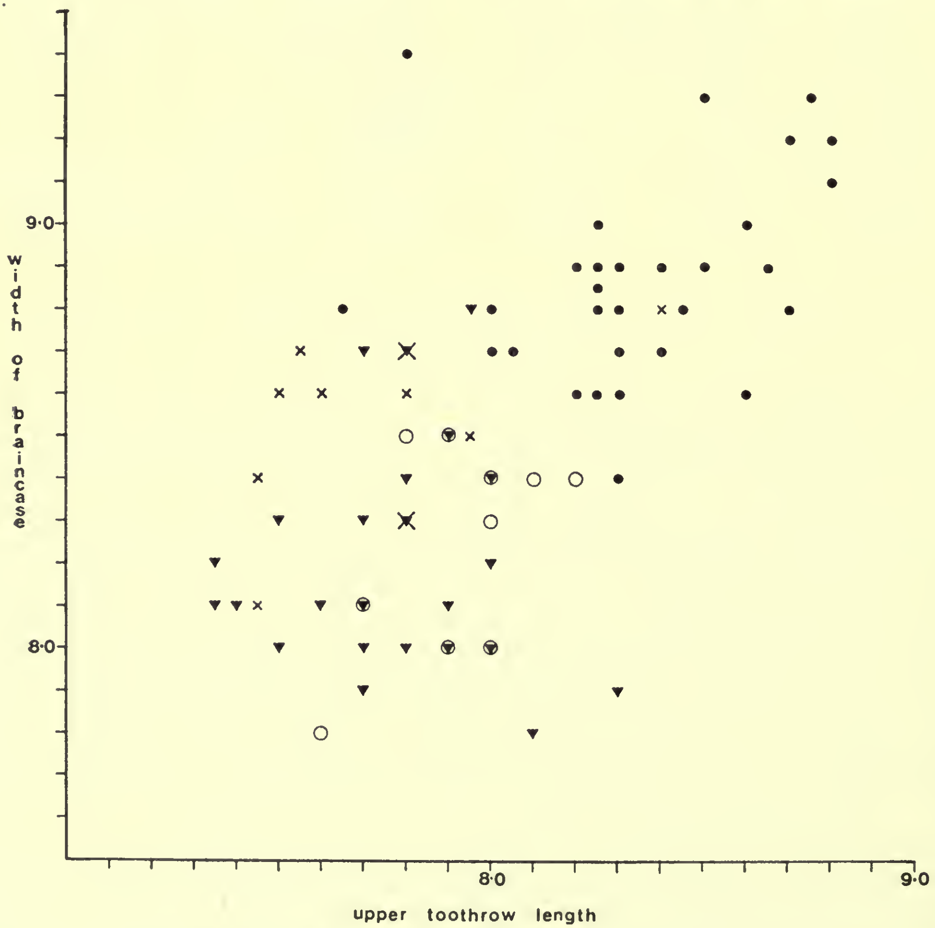

FIG. 10. Comparison of skull size.
C. russula (Asia and Corsica) ● ; *C. suaveolens* (Isles of Scilly, Greece, Russian Turkestan, Yunnan) ▼ ; *C. dsinezumi* ×; *C. zarudnyi* ○.

and others of the Asian subgroup of *russula* (Lebanon (24), Israel (25), Afghanistan (28) and Punjab (32) and also Corsica (17)) range from 2·25 to 5·48. Some of these are fairly low but since the sample populations are geographically well separated their similarity is unlikely to reflect any true relationship. Yunnan (42), for example, has D^2 values under 3·0 with Afghanistan (28), Corsica (17), Punjab (32), Lebanon (24) and Israel (25) ; Afghanistan has D^2 values under 3.0 with the Isles of Scilly (1), Russian Turkestan (30) and Yunnan (42).

Compared with Asian and Corsican *russula* these populations of *suaveolens* have somewhat smaller skulls (see Fig. 10 and Table 3) and shorter tails (TL 27–48 mm, $\bar{x}$ 35·3 mm ; in the Asian and Corsican *russula* TL 36–52 mm, $\bar{x}$ 44·79 mm).

Richter (1970) decided to treat the entire species of *C. suaveolens* as a third subspecific group of *C. russula*, the other two being *russula* and *gueldenstaedti*. He postulated that the *suaveolens* subspecies group is merely a 'steppe form' of the *gueldenstaedti* subspecies group and that *suaveolens* has only secondarily come to inhabit the area occupied by the *russula* subspecies group in western Europe. While it is true that some populations of *suaveolens* mentioned above are similar to some members of Richter's *gueldenstaedti* subspecies group, it is possible to distinguish the two species where they occur together. Furthermore, there is usually no difficulty in distinguishing *suaveolens* from the subspecies that Richter places in the *russula* subspecies group, especially where they are sympatric, so *C. suaveolens* should be treated as a separate species.

Crocidura zarudnyi Ognev, 1928
Crocidura pergrisea Miller, 1913

One OTU of *C. zarudnyi* from Pakistan (29) was entered in the CVA but several specimens from other localities were also examined. Because only two specimens of *C. pergrisea* were seen, they were not placed in the CVA but they have been examined and are briefly commented on here.

Specimens from Pakistan are currently regarded either as a distinct species, *C. zarudnyi* Ognev, 1928, type locality Baluchistan border (see Hassinger, 1970 ; Spitzenberger, 1971), or as a subspecies of *C. pergrisea* Miller, 1913 from Baltistan (see Ellerman & Morrison-Scott, 1966). The Pakistan (29) specimens are geographically fairly close to specimens of *C. suaveolens* from Russian Turkestan (30) and to Asian *russula* from Afghanistan (28) and Punjab (32), although they are probably ecologically isolated by the rocky, desert habitat and the surrounding mountainous terrain. The D^2 values between Pakistan (29) and Punjab (32) and Israel (25) are fairly low, 3·5, but the Pakistan specimens are most similar to those of *C. suaveolens* from Jersey and Sark (2) with a D^2 value of 2·94. Despite the similarity to various populations of *C. suaveolens* from Greece, Russian Turkestan, Yunnan, the Channel Islands and the Isles of Scilly, the only relevant comparison is with the Russian Turkestan specimens of *C. suaveolens* which have shorter tails on average (TL 27–40 mm, $\bar{x}$ 32·2 mm ; in *C. zarudnyi* 36–57 mm, $\bar{x}$ 49·2 mm). The shape of the upper premolar is similar to that of specimens of Asian *C. russula*, though it is slightly smaller (see Fig. 6).

Miller (1913) described four specimens from Skoro Loomba, Shigar, Baltistan (2900 m), giving them the name *C. pergrisea.* Ognev (1928) first used the name *C. zarudnyi* for a new species which he had formerly described under a preoccupied name (1921). This new species, represented by one specimen, was collected in East Iran on the Baluchistan border.

Ellerman & Morrison-Scott (1966) examined three specimens from Baluchistan which they believed to be *zarudnyi* and placed this as a subspecies of *pergrisea.* Lay (1967) allocated to *C. pergrisea* six specimens from Iran, which Hassinger (1970) re-identified as *C. zarudnyi.* Hassinger made a preliminary study of the *C. zarudnyi–pergrisea* group and concluded that they were distinct species. He also described a new subspecies, *C. zarudnyi streetorum*, from Afghanistan.

Richter (1970) tentatively assigned both *zarudnyi* and *pergrisea* to the subspecies group *gueldenstaedti* of *C. russula.* Spitzenberger (1971) gave measurements of three subspecies of *C. pergrisea* (the nominate form *C. p. pergrisea*, *C. p. serezkeyensis* Laptev, 1929 from the Pamirs and a new subspecies from Turkey, *C. p. arispa*) as well as *C. zarudnyi* and distinguished them from both *C. russula* and *C. suaveolens* by the light colour of the pelage and the relatively long tail. Gureev (1971) also recorded *C. zarudnyi* as a separate species from *C. pergrisea.* Hassinger (1973) amplified his previous discussion by comparing Afghan specimens with other species, still concluding that *C. pergrisea* and *C. zarudnyi* are two separate species. He distinguished *C. zarudnyi* from *C. russula* by its smaller size and from both *C. russula* and *C. suaveolens* by the relatively long tail and pale coloration. The habitat of *C. zarudnyi* in Afghanistan is reported to be drier than that of either *C. russula* or *C. suaveolens.*

TABLE 4

Comparison of various samples of *C. zarudnyi* with *C. pergrisea*

	Condylobasal length mm	Upper toothrow length mm	Width of braincase mm	Length of mandible-excluding I_1 mm	Source when not measured personally
C. zarudnyi					
holotype	18·8	8·3	8·3	—	Ognev (1928)
C. zarudnyi					
Pakistan	16·1–18·7	7·15–8·2	7·8–8·5	8·7–9·2	
n = 11	x̄ 17·6	x̄ 7·8	x̄ 8·3	x̄ 9·0	
C. zarudnyi					
Iran n = 2	17·4, 18·7	7·8, 7·9	8·0, 8·3	9·0, 9·2	
C. zarudnyi					
Punjab n = 1	—	7·5	—	8·9	
C. pergrisea arispa					
holotype Turkey	17·7	7·5	8·25	9·0	
C. p. pergrisea					
Baltistan original series	19·0–19·4	8·6	8·8–8·9	—	Miller (1913)
C. p. pergrisea					
Baltistan n = 2	19·2	8·4	8·8	9·6, 9·7	

Table 4 shows that Baltistan specimens of *C. p. pergrisea* (two specimens measured personally plus measurements from the original description) are distinctly larger in most characters than all populations of *C. zarudnyi*. On these criteria the holotype of *C. p. arispa* from Turkey should be placed in the latter group as *C. zarudnyi arispa*. Although the specimens from Baltistan might be considered as a montane form of *zarudnyi* and, despite the fact that three specimens are not an adequate sample from which to draw conclusions, they are probably best regarded as examples of a distinct species, *C. pergrisea*.

Although rather similar to the Asian subgroup of *C. russula*, specimens of *C. zarudnyi* may usually be separated on size (see Fig. 10 and Table 3) as well as colour and labial length of upper unicuspids (1·45–1·9 mm, x̄ 1·77 mm in *C. zarudnyi*; 1·8–2·3 mm, x̄ 2·16 mm in Asian *C. russula*). However, separation from *C. suaveolens* is not so easy, the only useful characters being the pale pelage colour of *C. zarudnyi* which is paralleled by several populations of *C. suaveolens* from Russian Turkestan, Algeria, Israel and also specimens from Central Gobi, Mongolia, described by Allen (1938) under the name of *C. ilensis lar* (which Ellerman & Morrison-Scott (1966) believed to be a subspecies of *suaveolens*). This character may reflect adaptation to local environment rather than phylogenetic affinity. The other character is the relatively long tail which is also not an exclusive character (ratio of TL : UTL 3·4–5·2 : 1 in *C. suaveolens*; 4·8–7·1 : 1 in *C. zarudnyi*). Both *C. suaveolens* and *C. zarudnyi* have been recorded from Iran (Lay, 1967), Turkey (Spitzenberger, 1970, 1971) and Afghanistan (Hassinger, 1970, 1973) but not from the same habitats, and while the mean skull size is usually greater for specimens of *C. zarudnyi* than *C. suaveolens* the only distinct character is the greater tail length of the former. The evidence suggests that *C. zarudnyi* is fairly closely related to *C. suaveolens* and may be simply an ecological form of it, but for the present it is retained as a distinct species.

Crocidura russula (Hermann, 1780)

The OTUs that belong to this species fall into two groups roughly equivalent to a geographical division into European and Asian forms, except that the Corsican (17) population appears to belong to the latter group and Algeria to the former. Apart from these anomalous OTUs the European group consists of Guernsey and Alderney (3), France (4), Spain (6), Portugal (7), Germany, Belgium and Holland (10), Switzerland (13), Sicily (15), Sardinia (16) and also Algeria (8); the Asian group includes Turkey (22), Lebanon (24), Israel (25), Afghanistan (28), Kashmir (31) and Punjab (32).

Fig. 11 gives the distribution of this species and shows the wide geographical separation of the two subgroups. The main characters for distinguishing these groups are the differences in relative tail length, length of the upper unicuspids (LLU 2·0–2·5 mm, x̄ 2·25 mm; TL 28–46 mm, x̄ 38·35 mm in the European/Algerian group; LLU 1·8–2·3 mm, x̄ 2·16 mm; TL 36–51 mm, x̄ 45·33 mm in the Asian group). The premolar in mainland European populations has a very broad, squarish lingual portion in comparison with the narrow lobed appearance

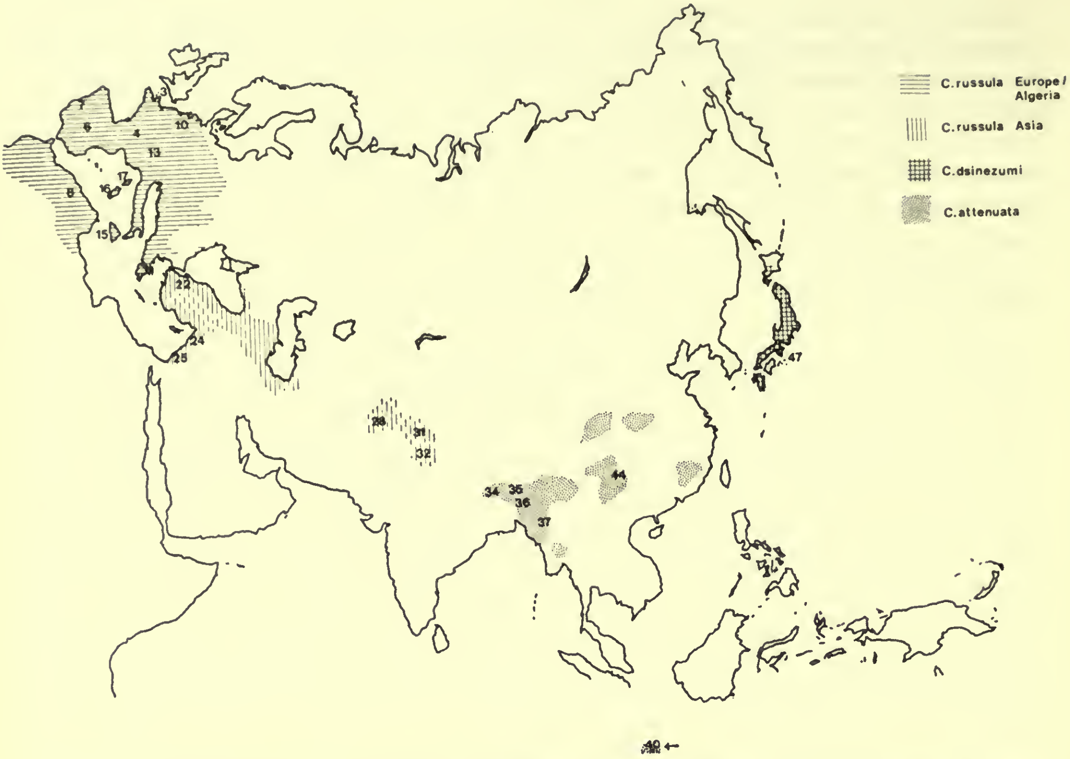

FIG. 11. Distribution of *C. russula, C. dsinezumi* and *C. attenuata*. Broken lines – exact distribution uncertain.

characteristic of the Asian subgroup and Corsica (see Figs 5, 6 and 7). Skull size in the Asian subgroup is also on average slightly smaller than in the European/ Algerian group, see Table 3.

OTUs of the European subgroup are fairly similar to each other with D^2 values of 1–3. In particular Spain (6) and Portugal (7) are very alike with a D^2 of 1·23, as are France (4) and Germany, Belgium and Holland (10) with a D^2 of 1·42. The Algerian population, although separated from the European mainland and Sardinia, is nevertheless very similar as reflected by the low D^2 values of 2·42–2·86.

As in *C. suaveolens* the greatest variation is shown by island populations, especially Sicily (15), Sardinia (16) and Corsica (17) where the D^2 values range from 3·92 between Sicily and Corsica, 3·95 between Sicily and Sardinia and 5·74 between Sardinia and Corsica. Specimens from Sicily have short narrow skulls in comparison with those from Sardinia which also have fairly well-spaced upper unicuspids (see Table 5). Specimens from Sicily are most similar to Spanish specimens with a D^2 value of 1·96, while those from Sardinia are closest to those from France and Germany, Belgium and Holland with D^2 values respectively of 2·14 and 2·2.

In spite of their close proximity to Sardinia and the European mainland, Corsican specimens show much more similarity to the Asian subgroup than to the European one. D^2 values between Corsica and the Asian subgroup are very low, varying from 1·44 to 2·33, while the lowest D^2 between Corsica and any member of the European group is 2·89 for Spain. The Corsican population is compared with those from Sicily and Sardinia in Table 5. However, the resemblance of the Corsican population to members of the Asian subgroup is unlikely to indicate a correspondingly close relationship. It is more likely to be allied to European mainland and nearby island populations despite the dissimilarity, which is probably a reflection of an isolated island population evolving along different lines.

TABLE 5

Variation between island populations of *C. russula*

	Corsica (n = 15)	Sicily (n = 5)	Sardinia (n = 9)
Condylobasal length, mm	17·5–19·1	18·0–18·3	18·3–19·1
	x̄ 18·10	x̄ 18·10	x̄ 18·75
Upper toothrow length, mm	7·7–8·7	8·1–8·3	8·3–8·9
	x̄ 8·21	x̄ 8·23	x̄ 8·62
Labial length of unicuspids, mm	1·9–2·3	2·1–2·2	2·3–2·5
	x̄ 2·06	x̄ 2·16	x̄ 2·42
Braincase breadth, mm	8·4–8·9	8·5–8·7	9·0–9·3
	x̄ 8·72	x̄ 8·63	x̄ 9·16
Tail length, mm	40–49	31–41	33–40
	x̄ 44·8	x̄ 35·0	x̄ 36·7

The Asian subgroup of *C. russula* has a wide distribution but shows very low D^2 values of 1–2. The adjacent Israel (25) and Lebanon (24) populations are very similar, with a D^2 value of 1·68, and although geographically separated, populations from Lebanon and Punjab (32) are also similar with a D^2 value of 1·83. Although geographically fairly close together Punjab and Kashmir (31) differ slightly, for while Punjab is fairly typical of the group Kashmir specimens are at the upper limit of the size range (e.g. UTL 7·4–8·7 mm, x̄ 8·25 mm for Punjab ; 8·6–8·8 mm, x̄ 8·73 mm for Kashmir).

The earliest name for the Asiatic group is *C. gueldenstaedti* Pallas, 1811 from the Caucasus. This form has been considered conspecific with European *C. russula* (from which it is geographically separated) by Kuzyakin (1944, 1965), Ellerman & Morrison-Scott (1966), Spitzenberger (1970), Felten, Spitzenberger & Storch (1973) and Richter (1970). The last placed East Mediterranean forms of *russula* in the same subspecies group as *gueldenstaedti*.

C. gueldenstaedti has been regarded as specifically distinct by Vinogradov (1958), Gureev (1971) and Kock (1974). Vinogradov presumably contrasted the structure of the external genitalia of both European *russula* and *gueldenstaedti*, although only producing evidence about the latter. The character he did use was the difference in relative tail length.

Without actually examining any specimens of *gueldenstaedti* from the Caucasus, I hesitate to use this name as the senior synonym of any of the subspecies listed here, although accepting its usage by other authors for *C. r. monacha* of Turkey as probably correct. For the same reason it seems incorrect to use it as a blanket name as Richter did, especially as some of the subspecies he included in that group appear fairly distinct. Also it is not necessarily correct to ally Asian forms with Mediterranean island forms which may have originated from any of many possible sources and which are presumably fairly isolated genetically. For example, although Corsican animals very closely resemble populations from Lebanon and Punjab they are also similar to Spanish specimens (see above, p. 293).

The following subspecies have been examined and fall into two groups ; European group

C. r. russula (Hermann, 1780). European mainland (4, 10, 13).
C. r. pulchra Cabrera, 1907. Spain, Portugal (6, 7).
C. r. peta Montagu & Pickford, 1923. Guernsey, Herm and Alderney (3).
C. r. ichnusae Festa, 1912. Sardinia (16).
C. r. sicula Miller, 1901a. Sicily (15).
C. r. cyrnensis Miller, 1907. Corsica (17).
Associated with this group is
C. r. agilis Levaillant, 1867. Algeria (8).
Asian group
C. r. monacha Thomas, 1906 (probably *C. r. gueldenstaedti* Pallas, 1811 see above). Turkey (22).
C. r. pullata Miller, 1911. Kashmir (31).

Also samples from Lebanon (24), Israel (25) and Punjab (32).

The affinities of *C. russula* and *C. suaveolens* have been discussed previously under *C. suaveolens* and those of *C. russula* and *C. leucodon* are dealt with in the account of *C. leucodon*.

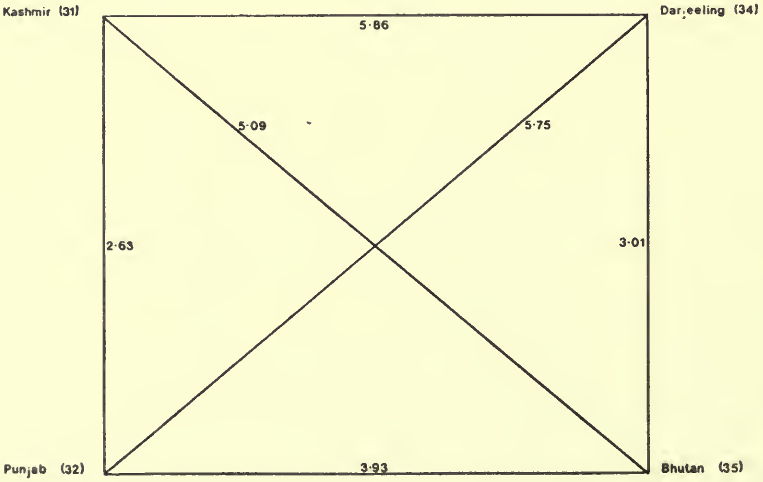

FIG. 12. D^2 values between the closest geographical populations of *C. russula* and *C. attenuata*.

C. attenuata may be distinguished from *C. russula* by the longer tail (TL 36–51 mm, x̄ 45·33 mm in Asian *russula*; 50–79 mm, x̄ 62·94 mm in *C. attenuata*). Kashmir (31) and Punjab (32) populations of the Asian subgroup of *russula* mark the eastern limit of this group, while Darjeeling (34) and Bhutan (35) are the westernmost populations of *C. attenuata*. The D^2 values between these four populations are shown in Fig. 12.

The lowest figure, which is between Punjab (32) and Bhutan (35), does not in this case represent great similarity as specimens from Punjab may usually be distinguished from Bhutan specimens by their slightly broader skulls and shorter tails (IB 4·2–4·5 mm, PB 6·0–6·4 mm, TL 40–51 mm in Punjab specimens of *C. russula*; IB 3·9–4·2 mm, PB 5·7–6·1 mm, TL 52–63 mm in Bhutan specimens of *C. attenuata*).

Crocidura dsinezumi Temminck, 1844

Specimens from Japan (47), currently regarded either as a distinct species, *C. dsinezumi*, or as a subspecies of *C. russula*, emerge in the CVA close to certain OTUs of both the Asian subgroup of *C. russula* and *C. suaveolens*. The Japanese specimens may be distinguished from their nearest neighbours of *C. suaveolens* occurring in Korea and Tsushima Islands, which are smaller, see Table 3. Although geographically well separated from other samples of *C. suaveolens*, the Japanese population shows low D^2 values with some OTUs, such as Jersey and Sark (2) and Greece (21), of 2·7. Low D^2 values are also shown between Japan and the Asian subgroup of *C. russula*, for example Punjab (32) with 2·7, Lebanon (24) with 2·8. The size of the skull is within the upper limits of *C. suaveolens* but only just within the lower limits of Asian *russula* (see Fig. 10), while the tail is relatively long and within the range of Asian *russula* (TL 37–50 mm, x̄ 44·6 mm).

The Japanese population was described as a distinct species, *C. dsinezumi*, but was treated as a subspecies of *C. russula* by Ellerman & Morrison-Scott (1966). Imaizumi (1970) regards *C. dsinezumi* as a distinct species and separable from *C. suaveolens* occurring in China, Korea and the Tsushima Islands. This view seems preferable and it is considered here to be a separate species.

Crocidura attenuata Milne-Edwards, 1872

This species includes the following OTUs: Darjeeling (34), Bhutan (35), Assam (36), Burma (37), China (44) and also Christmas Island (40). Specimens from Christmas Island have hitherto been assigned to *C. fuliginosa trichura*. The distribution of *C. attenuata* is shown in Fig. 11.

D^2 values between Darjeeling, Bhutan, Assam and China range from 2·43 to 3·47, which, while not as low as in some groups, nevertheless indicate a fairly high degree of relationship, especially when the geographical distances and variation in ecological conditions are taken into account. Darjeeling, Bhutan and Assam are at least partially isolated from each other by the mountainous terrain and separated from Burma and China by distance and differing habitats. The Burmese population is separated from any group other than *C. attenuata* by very high values of D^2. The lowest D^2 value is 4·84 with Assam and 4·91 with Darjeeling.

Christmas Island is a considerable distance from the main distribution area of *C. attenuata* but it shows relatively low D^2 values of 3·65–4·73 with Darjeeling, Bhutan, Assam and Burma. It shows no similarity to any other group entered in the CVA and may be readily distinguished from both the small and very large species of *Crocidura* occurring in Indonesia, which is the nearest area where shrews of this genus occur. A single specimen from Java and three from Sumatra closely resemble both Christmas Island specimens and other populations of *C. attenuata*, which suggests that this species may also be present, under different names and rarely recorded, in some parts of Indonesia. This would make the presence of *attenuata* in Christmas Island more likely, as a representative at the extreme limit of a species having a discontinuous distribution from Asia down through the Indonesian chain.

The Mahalanobis' distances are a reflection of the range of variation in this group, for example, in populations from Bhutan and Christmas Island the anterior part of the skull is fairly narrow (MB 5·2–5·9 mm, $\bar{x}$ 5·5 mm) but the posterior part of the skull in the latter population is wider than in the former (PB 5·7–6·1 mm, $\bar{x}$ 5·84 mm in Bhutan; 6·1–6·5 mm, $\bar{x}$ 6·32 mm in Christmas Island) – see Fig. 13. Measurements for the species are given in Table 6.

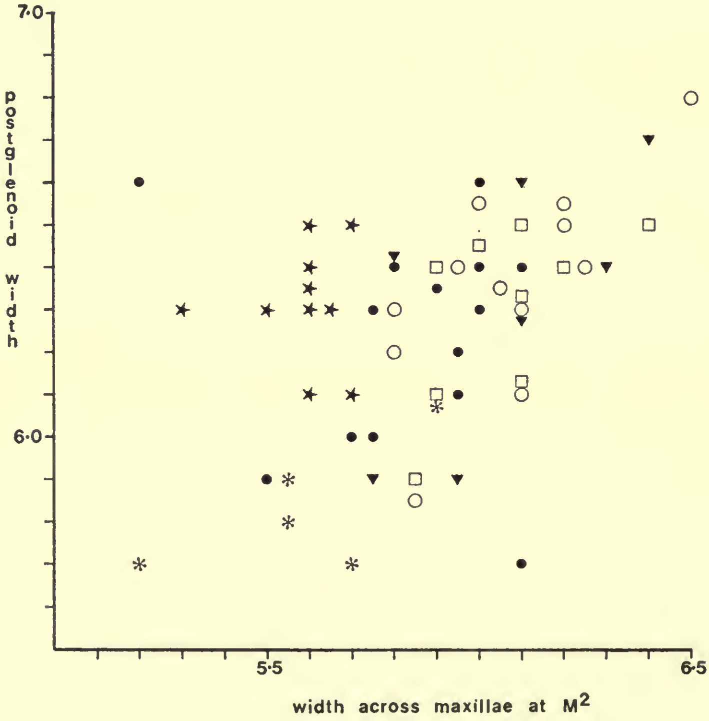

FIG. 13. Variation in skull width in populations of *C. attenuata*.
Darjeeling ●; Bhutan ∗; Assam ○; Burma □; China ▼; Christmas Island ★.

C. attenuata has apparently been confused with *C. fuliginosa* in the past and it seems likely that the latter name has been used at various times to refer to quite different animals. For example, Blanford (1888) synonymized *C. rubricosa* and *C. kingiana* (currently regarded as subspecies of *C. attenuata*) with *C. fuliginosa*, giving the distribution as Eastern Himalayas, Assam and Tenasserim (Burma). Thomas (1889) gave the distribution of *C. fuliginosa* as Himalayas through Burma to Java and in this paper Dobson described a new shrew from Christmas Island as a geographical race – *C. fuliginosa trichura*. The holotype and ten other specimens from Christmas Island are in the BMNH ; information given above indicates close association with *C. attenuata* and certainly none with the group referred to as *C. fuliginosa* in this report. The correct name for the Christmas Island *Crocidura* is thus *C. attenuata trichura*.

The following subspecies have been examined :

C. a. attenuata Milne-Edwards, 1872. China and Hainan (44).
C. a rubricosa Anderson, 1877. Assam, Himalayas (34, 35, 36).
C. a. trichura Dobson, 1888. Christmas Island (40) – formerly attributed to *C. fuliginosa trichura*.

Also a sample from Burma (37), an *attenuata* whose affinities are uncertain at subspecific level.

The affinities of this species with members of the Asian subgroup of *C. russula* have been discussed previously under the latter species. Key 3 (p. 282) and Fig. 7 give the characters for separating *C. attenuata* from *C. fuliginosa* and others occurring in the area.

TABLE 6

Size range of *C. attenuata*, *C. leucodon*, *C. lasiura* and *C. fuliginosa*

	Condylobasal length, mm	Upper toothrow length, mm	Width of maxillae at M^2, mm	Braincase breadth, mm
C. aitenuata Asia	18·3–20·6 x̄ 19·95	7·8–9·8 x̄ 8·79	5·2–6·5 x̄ 5·89	8·2–10·0 x̄ 9·12
C. leucodon France, Germany, Yugoslavia	17·8–19·9 x̄ 18·74	8·0–9·2 x̄ 8·60	5·7–6·5 x̄ 6·15	8·6–9·5 x̄ 9·11
Switzerland, Asia Minor	19·0–21·4 x̄ 19·96	8·8–10·2 x̄ 9·18	5·8–6·8 x̄ 6·29	8·8–10·2 x̄ 9·45
C. lasiura Korea	18·6–21·6 x̄ 20·77	9·2–10·3 x̄ 9·74	6·2–7·0 x̄ 6·85	9·1–10·2 x̄ 9·67
C. fuliginosa Asia, Malaysia	21·3–25·0 x̄ 22·80	9·4–11·5 x̄ 10·40	6·2–7·8 x̄ 6·90	9·5–11·1 x̄ 10·10

Crocidura leucodon (Hermann, 1780)

Fig. 14 gives the distribution of this species. The OTUs are : France (5), Germany (11), Switzerland (14), Yugoslavia (20), Turkey (23), Israel and Lebanon

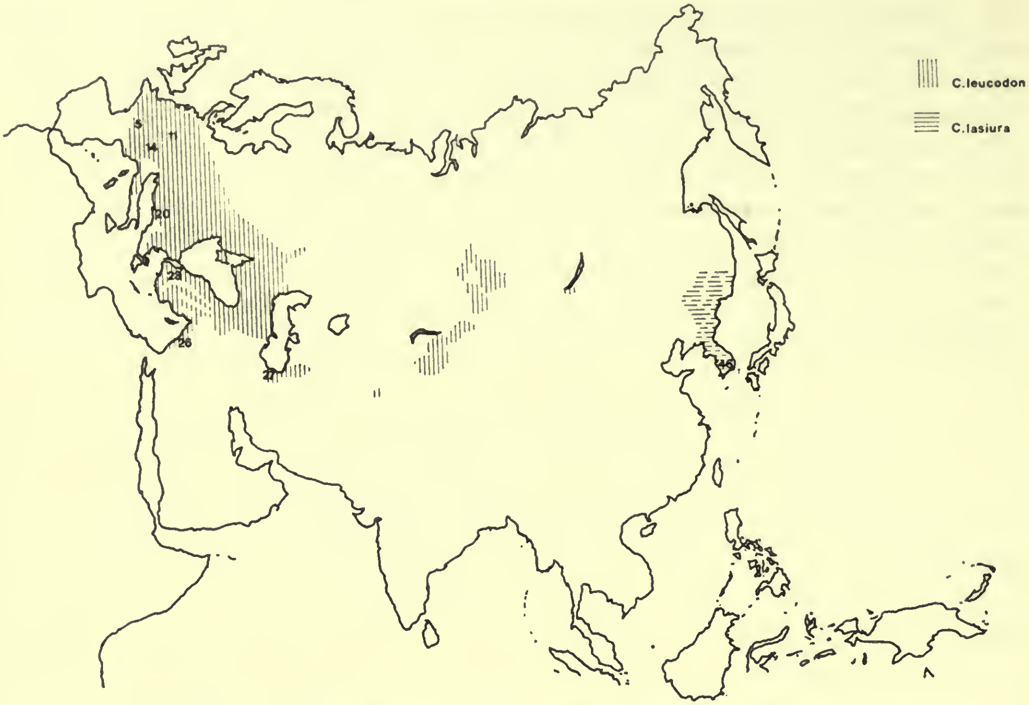

FIG. 14. Distribution of *C. leucodon* and *C. lasiura*. Broken lines – exact distribution uncertain.

(26) and also Iran (27) which has hitherto been regarded as a subspecies of *russula* – *C. r. caspica*.

This is a loosely knit group exhibiting a large range in variation. Those showing greatest association are European populations from France (5), Germany (11) and Yugoslavia (20) which have D^2 values between 1 and 3. French and German populations in particular have crowded unicuspids (LLU 1·8–2·1 mm, $\bar{x}$ 1·93 mm), while this measurement in the Yugoslavian population is 1·9–2·3 mm, $\bar{x}$ 2·05 mm. Skins usually show a sharp delineation along the flanks between the dark dorsal and pale ventral colour.

Although hitherto believed to belong to *C. russula*, Iranian specimens can be readily distinguished from that group – see last section of this species account. The Iranian population is very similar to that from Turkey with a D^2 value of 2·4. Both Iranian and Turkish specimens on average have larger skulls with uncrowded unicuspids in comparison with their European counterparts (LLU 2·1–2·55 mm, $\bar{x}$ 2·23 mm). Turkish specimens have a dark dorsum and paler venter although not so definitely bicoloured as European specimens, while Iranian specimens differ markedly in their very dark dorsal and ventral surface.

Specimens from Israel and Lebanon are most similar to those from Turkey and Iran, although the D^2 value is rather high. They fall within the range on skull size and the pelage colour resembles that of Turkish specimens.

Although Swiss specimens might be expected to be most similar to nearby populations from France and Germany, Mahalanobis' distances are from 3 to 4, while the D^2 values between Swiss and Turkish populations is 2·26 and between Switzerland and Iran 2·77.

Variation between the two subgroups is shown in Table 6.

Turkish specimens are associated with other OTUs in this group by D^2 values of 2–5 and they represent *C. leucodon lasia* which has a chequered history. It was originally described by Thomas (1906) as a subspecies of *C. leucodon*, though he later (1907) declared it distinct enough to be a full species – *C. lasia*. Bobrinskii *et al.* (1944) decided it was a subspecies of the Korean *C. lasiura*, an opinion with which Ellerman & Morrison-Scott (1951) concurred, although in the second edition Bobrinskii (1965) included it as a distinct species – *C. lasia*. Vinogradov (1958), examining the external genitalia, was unable to differentiate *lasia* from *C. leucodon* although *C. lasiura* was found to be distinguishable. Lay (1967) and Gureev (1971) also regard it as a subspecies of *C. leucodon* and this seems the best arrangement since it is fairly similar to, though relatively larger than, the European members of *C. leucodon*. It is quite similar to specimens of *C. lasiura* (D^2 value of 3·03) but the considerable discontinuity of distribution and Vinogradov's findings discourage the view that they might belong to the same species.

Specimens from Iran, including the holotype of *C. russula caspica*, are most similar to *C. leucodon lasia* from Turkey and other members of the *leucodon* group. In 1951 Ellerman & Morrison-Scott noted that *caspica* might represent *C. lasiura* (in which species they had placed *C. leucodon lasia*). However, Bobrinskii (1965), Lay (1967) and Richter (1970) placed it with *C. russula* in the *gueldenstaedti* subspecies group with a number of other subspecies which in this report belong to the Asian subgroup of *C. russula* and are readily distinguished from Iran specimens. Finally, Gureev (1971) included *C. r. caspica*, together with *C. r. monacha*, in synonymy with *C. gueldenstaedti*. This last seems very suspect since specimens of *C. r. monacha* from Turkey may be distinguished from Iran specimens on many characters (see Table 7). Despite the marked colour difference I believe these specimens from Iran should be regarded as a subspecies of *C. leucodon* – *C. leucodon caspica* – close to *C. leucodon lasia*.

Another subspecies, *C. leucodon persica*, also occurs in Iran. The holotype and one other specimen are in the BMNH. They resemble European members of *leucodon* in size and colour and are easily distinguished from Iran specimens of *C. l. caspica*. However, while all specimens seen of *C. l. caspica* are from low altitudes (the type series from under 25 m), *C. l. persica* appears to be a high altitude subspecies since the holotype was collected at 1980 m.

The resemblance of specimens from Israel and Lebanon to *C. russula* from Central Europe was noted by Thomas (1919) in his original description of *C. russula judaica*. In 1951 Ellerman & Morrison-Scott suggested the possible inclusion of this form with *C. lasiura* (along with *lasia*). Harrison (1963) considered it to be a local form of *C. leucodon* and this view is supported by the resemblance to specimens of *C. leucodon* from Turkey and Iran (see Table 7).

TABLE 7

Comparison of western Asian populations of *C. leucodon* with Asian and the most similar European populations of *C. russula*

	C. russula western Asia including *C. r. monacha* (Turkey)	*C. l. lasia* Turkey	*C. l. caspica* Iran	*C. l. judaica* Israel and Lebanon	*C. russula* Belgium, Germany, France Switzerland
Condylobasal length	17·5–19·5 x̄ 18·39	19·0–21·4 x̄ 19·99	19·4–20·4 x̄ 20·10	19·2–21·1 x̄ 20·07	17·7–20·1 x̄ 18·98
Upper toothrow length	7·6–8·8 x̄ 8·28	8·9–10·2 x̄ 9·29	8·8–9·4 x̄ 9·10	8·8–9·8 x̄ 9·26	8·1–9·1 x̄ 8·68
Width across maxillae at M^2	5·2–6·0 x̄ 5·65	6·2–6·8 x̄ 6·44	6·0–6·3 x̄ 6·17	5·8–6·8 x̄ 6·21	5·7–6·5 x̄ 6·01
Braincase breadth	8·4–9·4 x̄ 8·91	9·1–10·2 x̄ 9·53	9·2–9·8 x̄ 9·50	8·8–9·6 x̄ 9·13	8·5–9·5 x̄ 9·05
Ratio of tail to upper toothrow length	4·5–6·3 : 1 x̄ 5·48 : 1	3·7–4·9 : 1 x̄ 4·33 : 1	3·8–5·2 : 1 x̄ 4·7 : 1	3·6–4·5 : 1 x̄ 4·14 : 1	3·4–5·3 : 1 x̄ 4·43 : 1

The following subspecies have been examined and fall into two main groups :

C. l. leucodon (Hermann, 1780). Most of Europe (5, 11, 20).
C. l. persica Thomas, 1907. Elburz Mountains, Iran.
The second subgroup includes :
C. l. lasia Thomas, 1906. Turkey, Transcaucasia (23).
C. l. judaica Thomas, 1919. Israel and Lebanon (26).
C. l. caspica Thomas, 1907. S. coast of Caspian Sea, Northern Iran (27).

A sample from Switzerland (14) of uncertain affinity.

Keys 1 and 2 give the characters that are useful in distinguishing *C. leucodon* from other species occurring in the area. Despite the original naming of Iranian specimens as *C. russula,* they are particularly similar to specimens of *C. leucodon lasia* from Turkey mentioned above and can be readily distinguished from the Asian subgroup of *C. russula* by their more robust, longer and broader skulls. They are rather similar to the European subgroup of *C. russula.* but the skulls are on average slightly larger and the resemblance is unlikely to be a true indication of relationship. Table 5 gives a comparison of these populations.

Swiss specimens of *C. leucodon* are most closely associated in the analysis with Swiss specimens of *C. russula* at a very low D^2 value of 1·64 and with other European members of that species at D^2 values of 2–3. In Switzerland individual specimens of the two species are not readily distinguished from each other except on the basis of colour. Specimens of *leucodon* fall in the upper part of the *russula* size range (CBL 18·0–19·9 mm, $\bar{x}$ 19·01 mm ; BB 8·5–9·4 mm, $\bar{x}$ 9·13 mm in *russula* ; CBL 19·2–19·8 mm, $\bar{x}$ 19·5 mm ; BB 9·2–9·5 mm, $\bar{x}$ 9·38 mm in *leucodon*). This problem in Switzerland obviously requires very careful investigation into ecology, behaviour and genetics to try to establish the true relationship between these species.

Crocidura lasiura Dobson, 1890

The distribution of this species, represented in this report by the Korean population (46), is given in Fig. 14.

Korea is geographically isolated from Middle Asian populations of *C. leucodon,* yet the D^2 value between Korea and Turkey (23) is comparatively low, at 3·03. The range in skull size is similar for Korean and Turkish populations but on average Korean specimens have larger skulls, see Table 6. In Korean specimens the ventral pelage colour is only slightly paler than the dark dorsum, in contrast to the more marked differentiation in Turkish specimens.

In this study *C. lasiura* was represented by a large series from Korea, including the holotype of *C. l. thomasi.* In the CVA this sample showed some affinity to *C. leucodon lasia* (23) with a D^2 value of 3·03, but diverged more from *C. leucodon caspica* (27), a D^2 value of 4·77, and *C. leucodon judaica* (26) a D^2 value of 6·38. Ellerman & Morrison-Scott (1966) also noted this similarity but the evidence of dissimilarity in penis structure (Vinogradov, 1958) strongly suggests that it should be retained as a distinct species.

The subspecies examined was :

C. lasiura thomasi Sowerby, 1917. Korea (46).

See Key (p. 282) for comparison with other species in the surrounding area.

OTHER SPECIES RECORDED FROM THE AREAS OF STUDY BUT NOT INCLUDED IN THE ANALYSIS

The following species recorded from Eurasia are either absent from the collection or there are too few specimens for inclusion in the previous account.

C. hispida Thomas, 1913. Middle Andaman Island, Bay of Bengal. The BMNH houses the holotype, which is a very large animal, (CBL 27·4 mm) much larger than any of the species described in this account and with the tail longer than the head and body. It is also distinguished by its semi-spinous pelage.

C. andamanensis Miller, 1902. South Andaman Island, Bay of Bengal. No specimens apart from a small hair sample which differs from other species in that some of the hairs are flattened, although they are not so broad as the hairs of *C. hispida*, and there is no mention in the original description of the pelage being spinous. From the description of the holotype it appears to be comparable in size, though slightly smaller than *C. hispida* (CBL 25·6 mm).

C. nicobarica Miller, 1902. Great Nicobar Island, Bay of Bengal. No specimens apart from a small hair sample which contains flattened, broadened, hairs resembling those of *C. hispida* but less spinous. The condylobasal length of the holotype given in the original description is 27·0 mm.

C. miya Phillips, 1929. Sri Lanka. The skin and skull of the holotype are in the collection of the BMNH. The specimen is distinguished by the proportionately very long tail but in other respects it is very similar to *C. attenuata* (CBL 19·7 mm, UTL 8·7 mm, MB 5·9 mm, HB 79 mm, TL 88 mm).

C. caudata Miller, 1901a. Palermo, Sicily. No specimens examined. Kahmann & Einlechner (1959) believe that this is a subspecies of *C. russula*.

C. balearica Miller, 1907. Minorca, Balearic Islands. Kahmann & Vesmanis (1974) consider this to be a subspecies of *C. suaveolens*.

From the U.S.S.R. Gureev (1971) records the following species which I have not seen :

C. ognevi Stroganov, 1956. Altai.

C. pamirensis Ognev, 1928. Lake Drum vicinity, southern slopes of Pamir Mountain Range.

C. armenica Gureev, 1963. 14 km down river from Garni, Armenia.

C. dinniki Ognev, 1921. Stavropol'.

From Japan Imaizumi (1970) records :

C. orii Kuroda, 1924. Amami-Oshima, Riukiu Islands.

Preliminary examination of examples of the following forms recorded from Sumatra and Java by Chasen suggests that they represent *C. fuliginosa* :

C. villosa Robinson & Kloss, 1918. Sumatra. Holotype in BMNH.

C. brunnea Jentink, 1888. Sumatra, Java. Holotype of *C. b. brunnea* and ten specimens of *C. b. pudjonica* loaned by Leiden Museum.

C. brevicauda Jentink, 1890. Java. Holotype and fifteen specimens loaned by Leiden Museum.

C. orientalis Jentink, 1890. Java. Holotype and eight specimens loaned by Leiden Museum.

C. melanorhyncha Jentink, 1910. Java. Holotype and one other specimen loaned by Leiden Museum.

The following species recorded from the Malaysian region have also been subject to a preliminary examination and may be easily separated from *C. fuliginosa* by their small size (CBL 15·2–19·5 mm).

C. monticola Peters, 1870. Java, Borneo, Lombok, Sumbawa, Komodo, Flores, Sumba and ? Timor. There is only one specimen in the BMNH collections.

C. aequicauda Robinson & Kloss, 1918. Sumatra, Malay Peninsula. Holotype in BMNH.

C. beccarii Dobson, 1886. Sumatra. One damaged specimen only.

C. bartelsii Jentink, 1910. Java. Four specimens loaned by Leiden Museum.

C. maxi Sody, 1936. Java. One damaged specimen loaned by Leiden Museum.

C. minuta Otten, 1917. Java. Two badly damaged specimens loaned by Leiden Museum.

Of these *bartelsii* is probably conspecific with *monticola*. It is possible that *maxi* and *minuta* might also belong to this species, although more specimens are required to furnish any definite conclusions.

I have seen none of the remaining species listed by Chasen :

C. paradoxura Dobson, 1886. Sumatra.

C. neglecta Jentink, 1888. Sumatra.

C. weberi Jentink, 1890. Sumatra.

C. lepidura Lyon, 1908. Sumatra.

C. vosmaeri Jentink, 1888. Banka Island.

There are several unidentified specimens from Sulawesi which fall within the range of *C. fuliginosa* although this species has not previously been described from there. Laurie & Hill (1954) list the following species, none of which has been examined :

C. elongata Miller & Hollister, 1921. North eastern Sulawesi.

C. nigripes Miller & Hollister, 1921. North eastern Sulawesi.

C. rhoditis Miller & Hollister, 1921. North eastern Sulawesi.

C. lea Miller & Hollister, 1921. North eastern Sulawesi.

C. levicula Miller & Hollister, 1921. Middle Sulawesi.

C. tenuis (Müller, 1839). Timor.

Taylor (1934) records eight species from the Philippines of which the BMNH houses examples of only the first one :

C. grayi Dobson, 1890. Luzon and Benguet, Philippines. Holotype and two other specimens in the BMNH (CBL 18·6–20·0 mm, UTL 8·5–9·1 mm, BB 9·3–9·5 mm,

Table 8

Mahalanobis' distances. The 47 OTUs are numbered as in Table 1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0·0															
2	3·1	0·0														
3	4·9	6·4	0·0													
4	6·2	7·9	2·0	0·0												
5	6·2	7·6	4·8	4·4	0·0											
6	4·5	6·4	1·9	2·0	4·8	0·0										
7	4·4	6·4	2·0	2·5	5·5	1·2	0·0									
8	5·8	8·1	3·7	2·5	4·7	2·4	2·8	0·0								
9	3·6	5·3	6·3	7·1	6·1	5·9	5·9	6·3	0·0							
10	6·6	8·4	2·6	1·4	4·5	2·9	3·1	2·9	7·5	0·0						
11	5·5	6·9	4·9	5·2	2·8	5·2	5·3	5·4	5·3	4·9	0·0					
12	2·7	3·1	6·5	7·8	8·1	6·1	5·7	7·4	4·0	8·3	6·9	0·0				
13	6·0	7·5	2·7	2·0	3·5	2·6	3·3	3·0	6·8	1·8	4·3	7·6	0·0			
14	6·9	8·5	4·0	3·2	3·4	4·1	4·7	3·9	7·5	2·4	4·2	8·7	1·6	0·0		
15	4·6	6·5	2·7	3·0	4·7	2·0	2·6	3·3	5·6	3·3	4·9	6·2	2·7	3·8	0·0	
16	7·2	9·2	3·5	2·1	6·0	3·1	2·9	2·8	8·1	2·2	6·4	8·5	3·4	4·4	4·0	0·0
17	3·1	4·2	3·4	4·5	5·7	2·9	3·2	4·7	5·7	5·2	5·9	4·9	4·5	5·8	3·9	5·7
18	3·2	4·1	6·4	7·4	7·4	5·8	5·4	6·9	3·4	7·9	6·4	2·2	7·3	8·4	5·7	8·1
19	2·0	3·4	5·3	6·7	7·2	5·0	4·6	6·5	3·9	7·2	6·2	2·0	6·8	7·9	5·2	7·5
20	5·6	7·5	4·2	3·6	1·9	3·8	4·5	3·5	6·2	3·6	3·3	7·7	2·9	3·0	3·9	5·0
21	3·1	3·9	4·5	5·6	6·5	3·8	3·8	5·6	4·5	6·2	6·0	3·5	5·5	6·8	3·6	6·4
22	4·7	5·5	3·5	4·1	6·1	2·8	3·4	4·5	6·9	4·8	6·7	6·1	4·0	5·3	3·7	5·2
23	8·0	9·3	5·3	4·4	3·4	5·3	6·2	4·9	8·6	4·0	5·3	9·9	3·1	2·3	5·4	5·8
24	3·7	4·4	3·3	4·5	6·3	3·1	3·3	5·0	6·2	5·4	6·5	5·0	4·8	6·2	4·3	5·7
25	3·3	4·6	4·0	5·0	6·7	3·2	3·1	4·8	5·9	5·7	6·7	4·4	5·3	6·7	4·5	5·7
26	9·3	11·2	5·9	4·1	5·6	5·7	6·0	4·2	9·7	3·8	6·8	10·9	4·4	4·3	6·5	4·0
27	7·4	8·5	4·7	3·7	4·0	4·4	5·1	4·2	8·1	3·7	5·6	9·0	2·5	2·8	4·6	4·8
28	2·6	3·6	3·6	4·7	4·6	3·3	3·6	4·8	4·6	5·1	4·3	4·2	4·1	5·1	3·7	6·0
29	3·7	2·9	6·9	8·2	8·6	6·4	6·4	8·0	6·4	8·9	8·4	3·8	8·1	9·3	7·2	9·1
30	2·7	4·0	6·1	7·0	5·9	5·5	5·5	6·2	3·4	7·1	4·8	3·3	6·2	6·9	5·3	7·9
31	4·7	5·9	3·9	4·1	4·9	3·3	3·7	4·1	6·7	4·7	5·7	6·5	3·9	5·1	4·7	5·3
32	3·5	3·8	4·1	5·2	6·0	3·7	3·9	5·3	5·9	5·7	6·0	4·5	4·8	6·1	4·5	6·3
33	6·0	5·3	8·7	10·2	11·5	8·5	8·2	10·2	8·2	11·0	11·0	5·2	10·6	12·0	9·2	10·9
34	8·2	7·9	8·2	8·6	10·0	7·6	8·0	8·8	10·6	9·5	11·2	9·2	8·7	10·0	8·7	9·5
35	5·9	5·6	6·6	7·4	9·0	6·0	6·3	7·6	8·3	8·4	9·6	6·6	7·6	9·0	7·0	8·4
36	8·0	7·7	6·6	7·0	8·9	6·4	6·9	7·9	10·4	7·9	10·0	9·2	7·2	8·5	7·5	8·1
37	10·8	10·7	9·5	9·8	11·7	9·6	9·9	10·5	12·9	10·5	12·8	11·9	10·3	11·2	10·8	10·7
38	10·9	11·7	8·4	7·7	8·6	8·3	9·1	8·5	12·9	7·7	10·2	12·9	7·5	7·5	9·1	8·6
39	13·1	13·6	10·4	9·7	10·2	10·6	11·4	10·8	14·9	9·7	11·9	15·2	9·5	9·3	11·2	10·7
40	10·0	9·2	10·0	10·7	12·6	9·7	9·9	11·1	12·3	11·7	13·5	10·4	11·0	12·4	10·8	11·5
41	11·7	11·8	9·3	8·9	9·4	9·5	10·3	10·0	13·3	9·3	11·2	13·5	8·7	8·9	10·3	10·3
42	2·4	3·7	3·9	5·2	6·0	3·7	3·2	5·2	4·2	5·7	5·1	2·9	5·2	6·4	4·3	6·0
43	12·1	12·0	9·8	9·5	9·8	10·1	10·8	10·7	13·8	9·8	11·5	13·8	9·1	9·2	10·7	10·8
44	6·4	6·9	5·3	5·5	7·1	4·8	5·5	6·0	8·7	6·5	8·4	8·1	5·7	6·9	6·0	6·8
45	3·3	3·3	7·5	8·8	9·1	6·9	6·8	8·3	4·7	9·4	8·2	2·0	8·7	9·7	7·0	9·6
46	9·8	11·0	7·9	7·0	5·4	7·7	8·6	7·2	10·5	6·5	7·1	11·9	5·7	4·7	7·6	8·2
47	3·3	2·7	5·1	6·5	7·3	4·8	5·1	6·8	5·7	7·2	7·2	4·0	6·2	7·5	4·9	7·8

Table 8 (*Cont.*)

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
17	0·0															
18	5·1	0·0														
19	4·0	2·0	0·0													
20	4·8	7·1	6·7	0·0												
21	3·3	2·9	2·7	6·0	0·0											
22	2·0	6·4	5·5	5·3	4·1	0·0										
23	6·5	9·6	9·2	3·3	8·0	6·0	0·0									
24	1·3	5·5	4·3	5·7	3·6	2·0	6·9	0·0								
25	1·5	4·7	3·7	5·8	3·4	2·7	7·6	1·7	0·0							
26	7·7	10·4	10·0	5·0	9·1	7·2	4·4	7·9	8·1	0·0						
27	5·5	8·6	8·4	3·8	6·8	4·6	2·4	5·8	6·3	4·2	0·0					
82	2·1	4·3	3·6	4·1	3·0	3·3	6·0	2·8	3·0	7·7	5·2	0·0				
29	3·8	4·8	4·0	8·1	4·6	5·2	9·9	4·0	3·5	11·2	8·9	4·4	0·0			
30	4·6	3·0	3·4	5·5	3·8	5·8	7·9	5·4	4·9	9·4	7·3	3·0	5·0	0·0		
31	2·3	6·5	5·7	4·0	5·2	2·9	5·2	2·9	3·0	6·1	4·3	3·0	5·3	5·4	0·0	
32	1·4	4·9	4·2	5·4	3·4	2·3	6·7	1·8	2·1	8·1	5·5	1·9	3·5	4·3	2·6	0·0
33	6·5	6·4	5·4	10·9	6·5	7·5	12·8	6·1	5·8	13·6	11·7	7·4	3·8	7·9	8·3	6·5
34	5·7	9·6	8·8	9·3	7·9	5·3	9·7	5·6	5·7	10·7	8·3	7·4	6·1	9·5	5·9	5·7
35	3·9	7·2	6·4	8·4	5·5	3·9	9·3	3·5	3·7	10·3	7·9	5·6	3·9	7·5	5·1	3·9
36	5·1	9·5	8·6	8·3	7·3	4·4	8·3	4·8	5·5	9·4	6·9	6·7	6·7	9·3	5·2	5·2
37	8·4	12·5	11·4	11·1	10·7	7·9	10·8	7·9	8·5	11·2	10·0	10·0	9·2	12·4	8·2	8·7
38	8·4	12·8	11·9	7·8	10·7	7·7	6·3	8·7	9·2	7·4	6·6	9·2	11·1	11·6	7·1	8·8
39	10·6	15·0	14·2	9·7	12·9	10·0	7·8	10·9	11·6	9·2	8·5	11·4	13·4	13·7	9·4	11·0
40	7·9	11·1	10·3	12·1	9·5	7·4	12·3	7·3	7·7	13·1	10·8	9·6	7·4	11·6	8·6	7·8
41	9·0	13·5	12·7	9·1	11·4	8·4	7·4	9·1	10·0	9·1	7·5	10·0	11·3	12·5	8·0	9·3
42	2·9	3·1	2·2	5·5	2·7	4·2	7·7	3·0	2·7	8·3	6·7	2·2	4·1	3·4	4·1	2·8
43	9·5	13·9	13·1	9·7	11·8	8·8	7·9	9·6	10·5	9·7	7·9	10·3	11·7	12·8	8·5	9·6
44	3·5	8·2	7·3	6·3	6·2	3·0	6·7	3·6	4·1	7·9	5·5	5·2	5·9	7·7	3·4	4·0
45	5·3	3·0	2·9	8·6	4·1	6·5	10·8	5·6	4·9	12·1	9·9	5·1	3·4	4·1	7·1	5·2
46	8·4	11·6	11·2	5·2	10·1	8·0	3·0	9·1	9·6	6·4	4·8	7·9	11·6	9·4	7·1	8·6
47	2·8	4·6	3·8	6·8	2·8	3·5	8·3	2·9	3·3	10·1	7·2	3·2	3·2	4·7	4·9	2·7

	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
33	0·0														
34	7·8	0·0													
35	5·4	3·0	0·0												
36	8·5	2·7	3·6	0·0											
37	9·9	4·9	6·4	4·8	0·0										
38	13·6	7·7	9·3	6·4	8·4	0·0									
39	15·8	9·8	11·5	8·4	9·8	2·7	0·0								
40	7·6	3·7	4·2	4·7	4·7	10·4	12·2	0·0							
41	13·6	7·2	9·1	5·9	7·1	3·7	3·7	9·2	0·0						
42	6·2	8·0	5·7	7·5	10·4	10·7	12·9	9·7	11·4	0·0					
43	14·0	7·9	9·6	6·4	7·6	4·3	4·0	9·6	1·5	11·7	0·0				
44	8·2	3·3	3·5	2·4	6·1	6·3	8·5	6·1	6·4	6·2	7·1	0·0			
45	4·5	8·8	6·2	9·2	11·8	13·3	15·5	9·9	13·7	4·3	14·1	8·1	0·0		
46	14·7	11·0	11·1	9·8	12·1	6·1	7·2	13·9	7·7	9·9	8·0	8·3	12·5	0·0	
47	5·3	6·3	3·8	5·9	9·2	10·2	12·3	7·7	10·4	3·7	10·7	5·1	3·9	10·1	0·0

HB of holotype 68 mm, TL of holotype 51 mm). This species seems very similar to *C. attenuata.*

C. parvacauda Taylor, 1934. Cotabato, Philippines.
C. halconus Miller, 1911b. Mindoro, Philippines.
C. beatus Miller, 1911b. Mindanao, Philippines.
C. mindorus Miller, 1911b. Mindoro, Philippines.
C. grandis Miller, 1911b. Mindanao, Philippines.
C. palawanensis Taylor, 1934. Palawan, Philippines.
C. edwardsiana Trouessart, 1880. Jolo, Sulu Archipelago, Philippines.

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BIOLOGY AND FINE STRUCTURE OF *CRYPTODIFFLUGIA OVIFORMIS* (RHIZOPODEA : PROTOZOA)

R. H. HEDLEY, C. G. OGDEN
AND
N. J. MORDAN

BULLETIN OF
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RONALD HENDERSON HEDLEY, COLIN GERALD OGDEN
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SYNOPSIS

Cryptodifflugia oviformis, a cosmopolitan freshwater, moss and soil inhabiting testacean has been established in clonal culture with a doubling time of between 29 and 41 hours ; it is capable of reproducing in a 14 parts per thousand saline solution. The shell is shown to have two components, a thin outer organic layer and a thick inner, non-crystalline calcareous layer. The process of reproduction by simple division and the fine structure of the vegetative stage are described in detail. Ultrastructural features of special interest are the presence of calcareous inclusions in the mitochondria ; and a storage area for polysaccharide material within the cytoplasm.

Cryptodifflugia operculata of Page (1966) is considered to be a synonym of *Cryptodifflugia oviformis* Penard (1890).

INTRODUCTION

THE main characters used in the classification of testate amoebae are the form, structure and composition of the shell and the form of the pseudopodia. The shells are generally reported as being either purely organic, arenaceous, or siliceous with occasional reports of forms secreting calcareous shells being unsubstantiated. Until relatively recently information on the biology of many testate amoebae has been known only from infrequent observations on living animals, usually isolated as individuals during ecological or faunal surveys of freshwater habitats. The establishment and study of clonal cultures in this laboratory of certain species with siliceous shells (Hedley & Ogden, 1973, 1974a ; Hedley *et al.*, 1974) have contributed to our understanding of their biology and shell structure.

Recent ultrastructural studies on arenaceous forms (Netzel, 1972a; Eckert & McGee-Russell, 1974) and on organic forms (Griffin, 1972; Netzel, 1972b, 1975a, b) have contributed towards the understanding of their shell formation.

Species attributed to the genus *Cryptodifflugia* Penard, 1890, are possibly the smallest and most widely distributed of testate amoebae. There has been some doubt amongst protozoologists regarding the structure and composition of the shell in these animals with previous descriptions (Penard, 1890; Deflandre, 1953; Grospietsch, 1964; Page, 1966) reporting it as chitinous, smooth, hyaline and rigid.

The present work describes some aspects of the biology and shell structure of *Cryptodifflugia oviformis* Penard, 1890, an unusual testacean in that it is now reported as possessing a calcareous shell.

Previous work – taxonomy

The genus *Cryptodifflugia* was erected by Penard (1890) for the reception of a new species *C. oviformis*. Penard (1902) later amended his initial description and described two further species, *C. compressa* and *C. sacculus*. These three species were redescribed and illustrated by Playfair (1917) with five new species, *C. minuta*, *C. angulata*, *C. valida*, *C. crenulata* and *C. pusilla*, and four varieties, all from ponds or swamps in Australia. Zacharias (1903) reported a new species, *C. turfacea*, which sometimes had two apertures each having a distinct rim or collar. Another new species, *C. voigti*, described by Schmidt (1926) was observed to have an apertural rim and particles adhering to the shell surface.

Deflandre (1953) emended the generic diagnosis of both *Cryptodifflugia* Penard, 1890 and *Difflugiella* Cash, 1904, using the degree of compression of the shell as a main character. These emendations included the transfer of the type species, *C. oviformis*, of the genus *Cryptodifflugia* to the genus *Difflugiella*. Several authors, Bonnet & Thomas (1955, 1960), Thomas (1959), Grospietsch (1964) and Schönborn (1965), have agreed with Deflandre's changes. For example, Thomas (1959) redescribed *D. oviformis* (Penard, 1890) and tabulated the previously reported measurements of this species. In a review of the genera *Cryptodifflugia* and *Difflugiella*, Grospietsch (1964) agreed with Deflandre (1953) and gave keys to the species of both genera. Whilst Schönborn (1965) described four new species of *Difflugiella* and redescribed *D. crenulata* (Playfair, 1917), *D. oviformis* (Penard, 1890) and *D. voigti* (Schmidt, 1926).

Page (1966) reviewed the genus *Cryptodifflugia* and concluded that Deflandre's emendations were unjustified. He based his opinion on the original descriptions of *Difflugiella* and *Cryptodifflugia* which showed the former to have a flexible shell, whilst the latter had a rigid shell. Recent ultrastructural studies on *Difflugiella* sp. by Griffin (1972), and the present work, support the view that this feature is a good taxonomic character.

Page (1966) used the presence of an operculum in the aperture of encysted animals of a new species *C. operculata* to distinguish it from *C. oviformis*. This feature had not been previously described and it is difficult to determine whether its omission in earlier descriptions was due to oversight, as the operculum is often difficult to see with the optical microscope, or to the absence of encysted animals in the material examined by other authors.

As a result of an examination of the two available cultures of *C. operculata* and *C. oviformis* (from this laboratory), Dr Page has suggested in a personal communication that the presence of an operculum may not be a good specific character, as it appears to be present in most encysted animals. Our own studies show that the structure of the shell and the fine structure of the cytoplasm in the two forms are indistinguishable. It is suggested therefore that *C. operculata* be regarded as a synonym of *C. oviformis*.

Previous work – biology

In his original description of *Cryptodifflugia oviformis*, Penard (1890) reported that the cytoplasm filled the shell and contained one nucleus, a contractile vacuole close to the nucleus and 'numerous brilliant granules'. Similar 'brilliant' or 'coarse' granules found in *C. operculata* have been shown by Page (1966) to react positively with supravital Janus green from which he concluded that they are mitochondria.

Penard (1890) observed that the form of the small number of pseudopodia of *C. oviformis* changed rapidly and later (Penard, 1902) described the pseudopodia as straight structures without ramifications. The arrangement and length of the pseudopodia in *C. oviformis* are described by Schönborn (1965), who also observed that the rate of locomotion varied from 34 to 40 μm/min. According to Page (1966) there are between two and five pseudopodia in *C. operculata* that extend from a mass of cytoplasm outside the aperture. Both this mass and the cytoplasm appear to be free from coarse granules. Although these pseudopodia appear to be filose all seem to have rounded ends. The rate of locomotion of ten individuals ranged from 14 μm/min to 28 μm/min.

United individuals were described as 'conjugating tests' by Penard (1902) in which one shell always appears empty whilst the other shell, usually the larger, contains a rounded mass of cytoplasm separated from the aperture by a 'chitinous' diaphragm. Penard suggests that this could be a resting stage during which the animal constructs a new shell that gradually hardens. Playfair (1917) has described similar united individuals of *C. oviformis* as encysted forms. The process of binary fission has been described for *C. operculata* by Page (1966), in which most of the cytoplasm to form the daughter cell is extruded before nuclear division begins and is followed by the formation of a new shell around the daughter. Nuclear division from prophase to anaphase takes place in the aboral region of the parent and the daughter nucleus moves into the extruded cytoplasm in late telophase. Both the nuclear membrane and the nucleolus disappear before metaphase and no centrioles are seen. It also appears that most of the granules pass into the extruded cytoplasm and few are left in the parent.

Penard (1890, 1902) described an encysted form of *C. oviformis* in which the cytoplasm was concentrated and contained in the aboral region behind a cyst-membrane. A similar cyst has been described by Schönborn (1965). Page (1966) reported this type of cyst only once in *C. operculata*, but regularly found cysts in which the aperture was sealed. In these latter forms the cytoplasm filled the shell, the contractile vacuole disappears and the aperture is blocked by a lens-shaped operculum. At encystment the operculum is either rejected from the shell or ingested within the cytoplasm.

MATERIALS AND METHODS

Cryptodifflugia oviformis was isolated from a sample of moss, *Eurhynchium praelongum*, taken from the bark of a tree at Cilpost Farm, Whitland, Carmarthenshire, Wales, in July 1968. Rough cultures were obtained by allowing small portions of this sample to stand, covered by a shallow layer of culture medium, at room temperature 18–20 °C. Agnotobiotic cultures were kept in small plastic containers on a thin substrate of agar (1 per cent agar agar in distilled water) with a sterilized wheat grain added prior to setting and covered with a layer of culture medium. The medium was a 5 per cent (w/v) solution of sterilized soil extract in distilled water. Clonal cultures were established by isolating single active animals, and one such clone has been used subsequently to produce the working cultures. This clone has been deposited with, and is now maintained at, the Culture Centre of Algae and Protozoa, The Natural Environment Research Council, Cambridge, England (Reg. No. 1514/2).

Specimens of *C. operculata* obtained from the Culture Centre for Algae and Protozoa (Reg. No. 1514/1), which were initially isolated by Page (1966), have been maintained in a manner similar to *C. oviformis*. Under these conditions *C. oviformis* remains active for approximately 4 weeks, after this time mobility decreases and encysted forms predominate. Cultures may also be maintained on an agar agar substrate, streaked with the bacterium *Klebsiella pneumoniae*, but without a covering fluid. Such cultures, kept on agar slopes in closed universal bottles at 9 °C, may be sub-cultured successfully after 6 months (Dr F. C. Page, personal communication).

Cultures have been established using a graded (v/v) series of seawater to freshwater culture medium as the overlying culture fluid to the normal agar substrate. The initial experiments were made with 1, 2, 5 and 10 per cent seawater to freshwater mixtures, and in all cases active reproducing animals were observed. In subsequent experiments with higher concentrations of seawater it was found that cultures could be maintained in media up to and including 40 per cent seawater, which is the equivalent of a 14 parts per thousand saline solution.

Optical microscopy

Live animals were examined by both phase-contrast and bright-field illumination.

Scanning electron microscopy

Specimens taken from 4 or 5 weeks old cultures were cleaned by taking them individually through several changes of distilled water, using a single-hair brush.

They were allowed to dry and then transferred onto a previously cleaned cover-slip. These prepared cover-slips were mounted on a standard Stereoscan stub using an electrically conductive paint, 'Silver Dag', prior to being coated evenly with gold. The stubs were examined on a Cambridge Stereoscan MkII operating at 10 kV and the results recorded on Ilford HP4 film.

Preparations to display pseudopodia were obtained by fixing specimens *in situ* using the following method. The agar substrate in a culture vessel was wetted with a minimal quantity of culture medium, and a small number of specimens from a fresh culture were placed on this surface. After a short time the animals resumed their normal activities. The vessel was then quickly flooded with 3 per cent glutaraldehyde in cacodylic acid buffer, and left for 15 minutes. The agar surface was washed with the same buffer and selected squares were cut out and allowed to air dry. These squares were mounted on a standard Stereoscan stub using Araldite and processed as previously described.

Specimens from a culture vessel were air dried on pieces of spectographically standardized carbon rod for the analysis of inorganic chemical elements. Previous trials with this carbon rod had shown that it gave a minimal elemental background count. The pieces of rod were attached to Stereoscan stubs with Araldite. Stubs were then examined in a Cambridge Stereoscan coupled to an Ortec solid-state energy dispersive X-ray analyser, operating at 15 kV for 400 or 1000 seconds.

Electron probe analysis was carried out on specimens taken from a culture vessel and allowed to air dry onto a Stereoscan stub with a short shaft. They were coated with a thin layer of carbon and examined in a modified Cambridge Geoscan, operating at 20 kV with a specimen current of $0{\cdot}1 \times 10^{-7}$ amps.

Transmission electron microscopy

Specimens taken from cultures, approximately 2 or 3 weeks old, were fixed at room temperature for 12 minutes in 1 per cent glutaraldehyde in 0·025 M cacodylic acid buffer, followed by 7 minutes in 3 per cent glutaraldehyde in the same buffer. After several rinses in 0·1 M cacodylic acid buffer, they were post-fixed for 12 minutes in 1 per cent osmium tetroxide in distilled water. Some specimens were conventionally fixed, but before dehydration were treated with a chelating agent, 5% EDTA, for 15 minutes. The material was dehydrated, and embedded in Epon 812. Sections were cut on a Porter Blum MT2 ultramicrotome using a Du Pont diamond knife, stained in a saturated alcoholic solution of uranyl acetate and Reynold's lead citrate, and examined in an AEI 6B electron microscope operating at 60 kV. The results were recorded on Ilford EM6 plates.

The periodic acid/thiosemicarbazide/silver proteinate technique (Thiery, 1967) was carried out on thin sections mounted on gold grids. After treatment with 1 per cent periodic acid for 20 minutes at room temperature followed by several washes in distilled water, the sections were left for either 40 minutes or 18 hours in a 1 per cent solution of thiosemicarbazide in 10 per cent acetic acid. They were washed thoroughly in several changes of 10 per cent acetic acid followed by several rinses in distilled water, before treatment with 1 per cent solution of silver proteinate for 30 minutes in the dark. The grids were washed in distilled water before examination.

Thick, unstained sections, coated with carbon, were analysed for elemental composition in an AEI EMMA-4 analytical electron microscope, equipped with a minilens, operating at 80 kV with a probe size of 0·06 μA.

DISTRIBUTION

C. oviformis is commonly found in damp and wet mosses, standing water, on aquatic plants, various soils and forest litter. A list of locality records and references was given by Bonnet & Thomas (1960). Additional localities were given by several authors, Hoogenraad & Groot (1952), Štěpánek (1963) and Bonnet (1966).

The following list shows the geographically widespread distribution :

Europe :	England, Wales, Scotland, Ireland, France, Belgium, Holland, Germany, Iceland, Lapland, Italy, Czechoslovakia, Hungary, Bulgaria, Russia.
North America :	United States of America and Canada.
South America :	Columbia and Chile.
Africa :	Cameroun and the Congo.
Asia :	Siberia.
Australasia :	Australia and New Zealand.

SHELL STRUCTURE AND COMPOSITION

Based on measurements from a hundred specimens the ovoid, rigid and smooth shells of *C. oviformis* vary in length from 14·5 to 22·2 μm and in diameter from 12·8 to 17·6 μm. The single, terminal and circular aperture has a diameter of between 3·2 and 6·4 μm and is surrounded by a thin collar (Pl. 1, fig. A).

Ultrastructural observations show that the shell wall varies in thickness, between individuals, from 150 to 260 nm and that it is divided into two distinct layers. A thin outer organic layer, which is usually no more than 20 nm thick, and a thick inner layer of electron-dense calcified material. These layers appear to have a uniform thickness over most of the shell surface (Fig. 1), but in the apertural region there is a slight thickening of the calcified layer and an extension of the organic layer to form a circular collar (Fig. 2). This organic collar is strengthened at the internal face by a continuation of the calcified layer (Pl. 1, fig. B). Examination of the complete shell wall at the ultrastructural level is difficult because the calcified layer is not penetrated by the embedding resin, and as a result is either fractured or torn in thin sections (Pl. 2).

Whole shells, examined with an Ortec X-ray analytical attachment to the Stereoscan, showed significant elemental peaks for silicon, potassium and calcium, the last mentioned being pronounced. Semi-quantitative electron probe microanalysis of shells indicated that the calcium count-rate was high, and demonstrated a weak line for silicon corresponding to not more than 1 per cent. Sectioned material examined with the X-ray analytical electron microscope, EMMA, using a standard of calcium carbonate, gave significant intensities from the calcified layer. This

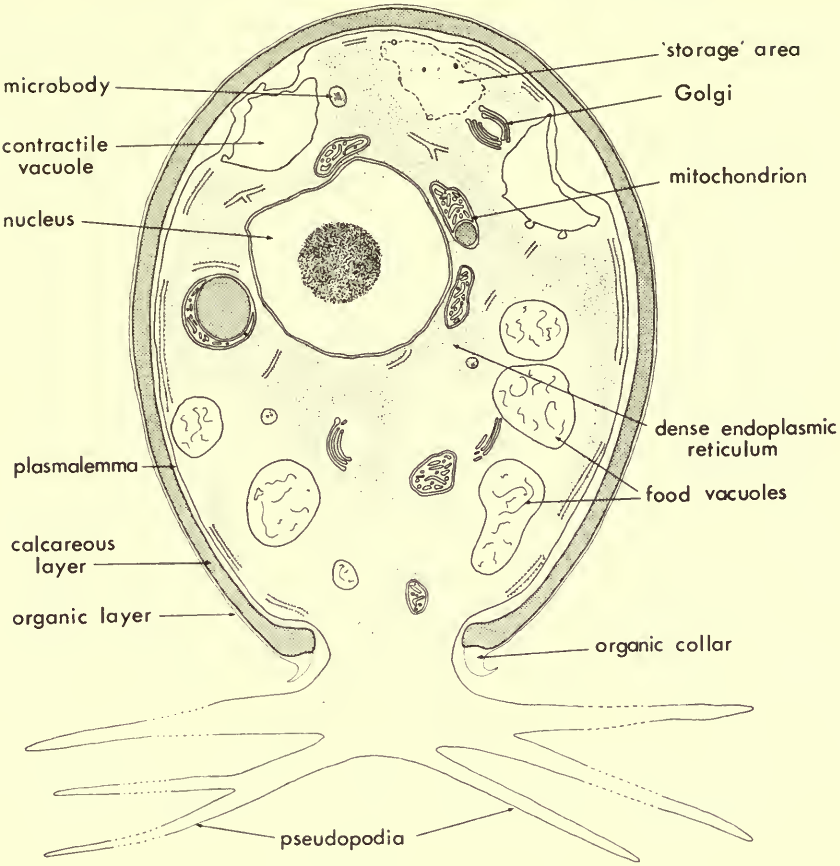
'storage' area
microbody
Golgi
contractile vacuole
mitochondrion
nucleus
dense endoplasmic reticulum
food vacuoles
plasmalemma
calcareous layer
organic layer
organic collar
pseudopodia

FIG. 1. Diagram of the vegetative stage of *C. oviformis* showing the arrangement of the main organelles.

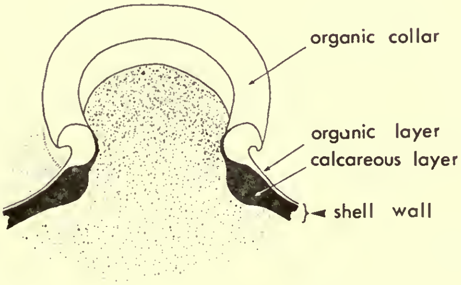
organic collar
organic layer
calcareous layer
shell wall

FIG. 2. Diagram of the apertural collar with a section cut away to show the relationship of the organic and calcareous layers.

layer also gave significant intensities for phosphorus, using sodium dihydrogen orthophosphate as a standard. Further attempts to analyse the composition of the calcified layer, using whole shells for X-ray diffraction and sectioned specimens for electron diffraction, were inconclusive but suggest that this material is mainly amorphous. Dr K. M. Towe (Smithsonian Institution, Washington, D.C., U.S.A.), who kindly undertook the electron diffraction analysis, suggested that the material was either amorphous or exceptionally beam-sensitive as it was unstable. He ruled out the possibility of the beam sensitivity being associated with the presence of an oxalate because there was no inversion to calcium oxide. In conclusion, we suggest that in all probability the calcified layer is amorphous calcium phosphate.

When whole specimens are immersed in either dilute nitric or hydrochloric acids or with 5% EDTA the major part of the shell dissolves. That which remains is the thin organic layer, delimiting the shape of the shell, and the organic thickening in the apertural region. In an attempt to demonstrate the fine structure of the organic layer, animals were fixed normally but before dehydration were decalcified by treatment with 5% EDTA for 10 minutes (Pl. 1, fig. C). The organic layer revealed by this method is a membrane-like structure which is thickened and folded at the aperture to form a collar (Pl. 1, fig. D). Specimens stained with the periodic acid/thiosemicarbazide/silver proteinate technique to demonstrate reactive hydroxyl groups show that the organic layer is composed of two thin, closely opposed, distinct membrane-like structures (Pl. 1, fig. E), with a high carbohydrate content.

Abnormal forms occur in cultures and represent about 3 per cent of the population. These are usually large forms, two or three times the size of a normal animal, and have two or more apertures (Pl. 1, fig. F). The shell of these animals is characterized by an uneven distribution and thickness of the outer organic covering (Pl. 1, fig. F; Pl. 6, fig. C).

CYTOPLASM

The cytoplasm normally occupies the whole of the shell cavity (Fig. 1; Pl. 2) and is enclosed by a plasmalemma. The single nucleus is normally spherical, between 4·3 and 5·1 μm in diameter, and is enclosed by two tripartite membranes. The nuclear matrix is granular with small, densely stained concentrations of chromatin scattered throughout and a dense nucleolus that is usually situated centrally. The nucleus is surrounded by a densely stained mass of granular endoplasmic reticulum (Fig. 1). This region of endoplasmic reticulum appears more electron-dense than the surrounding cytoplasm due to the concentration of ribosomes. Two or three contractile vacuoles may be present in the mid-body region (Pl. 3, fig. A). The area surrounding these vacuoles is free of ribosomes but has numerous small vesicles which are often continuous with the lumen of the vacuole. The contractile vacuoles lie at the periphery of the cytoplasm and discharge directly into the shell cavity. Specimens in 2-week-old cultures discharged their contractile vacuoles at periods that ranged from 25 to 33 seconds between systole and diastole. These periods increased in animals from 6-week-old cultures to range from 28 to 41 seconds. Numerous food vacuoles, which have a single unit membrane and may contain food organisms or waste material, occupy the apertural end of the cytoplasm (Pl. 2).

The mitochondria are ovoid or spherical, with tubular cristae, a dense granular matrix and they are distributed at random throughout the cytoplasm. Frequently large, spherical, electron-dense inclusions occur between the outer and inner mitochondrial membranes (Pl. 3, figs A and B). These inclusions are naturally electron-dense in sections from specimens fixed in glutaraldehyde but without subsequent treatment with heavy metals, and show similar fracture patterns to those sometimes seen in the electron-dense shell wall. We believe that these mitochondrial inclusions are the 'brilliant' or 'coarse' granules described by earlier workers. Analysis of these inclusions using the X-ray analytical electron microscope EMMA gave significant intensities for calcium and phosphorus which correspond to those produced by the shell. These calcareous inclusions dissolve in 5% EDTA.

As many as 6 Golgi bodies may be present in one animal and they are usually associated with concentrations of granular endoplasmic reticulum. Each dictyosome is composed of a stack of 3 to 6 saccules (Pl. 3, fig. C) which are usually concave and centrally flattened, whilst the matrix around these saccules may be noticeably less dense than the surrounding cytoplasm. Condensations of a substance, which is electron-dense with normal staining procedures, occur in the central areas of the saccules. This material appears as if it may pass to the outer margins of the saccules where they form spherical protrusions, which are budded off as smooth membrane-bound vesicles (Pl. 3, fig. C). At the inner face of the dictyosome, vesicles containing an electron-lucent material are formed (Pl. 3, fig. E). These vesicles are slightly larger than those containing electron-dense material and are lined by a thin layer of an electron-dense material (Pl. 3, fig. D). A third type of vesicle is often present in the dense granular endoplasmic reticulum (Pl. 4, fig. A). These vesicles are large, usually have electron-lucent contents, but are occasionally seen to contain an electron-dense material (Pl. 4, fig. D), and are often surrounded by a band of endoplasmic reticulum. Similar vesicles to these have been previously reported in *Trinema lineare* (Hedley & Ogden, 1974a).

On the basis of their distribution within the cytoplasm it is postulated that these three types of vesicles move through the cytoplasm along two distinct pathways. The large electron-lucent vesicles would pass through the central cytoplasm, whilst the smaller vesicles would pass around the less dense peripheral region to become incorporated at sites that are considered to be possible storage areas (Pl. 4, figs B and D). In the trophic animal there may be as many as three such storage areas, usually found on a level or posterior to the nucleus in the aboral region (Pl. 4, fig. C). These regions are electron-lucent and do not appear to have any limiting membrane.

When sections are treated with the periodic acid/thiosemicarbazide/silver proteinate technique the storage areas stain strongly, which might suggest that they are regions rich in carbodyrate. The small electron-lucent vesicles also contain the stain, but in these it is confined to the lining of the vesicles (Pl. 4, fig. B). The saccules of the Golgi apparatus are sometimes stained, as are the vesicles that are detached at their margins, but this staining is less positive (Pl. 4, fig. B). Similar results after using this technique were obtained from specimens which had been decalcified with EDTA prior to embedding.

Microbodies are present in most of the specimens examined. They are oval or spherical, varying between 0·25 and 0·44 µm in diameter, have a dense matrix and a single unit membrane. They may contain either one or two tubular-like elements, between 19 and 24 nm in diameter (Pl. 4, fig. E), or a rectangular structure of parallel lines with a spatial distance of 8 nm between each line (Pl. 4, fig. F). Similar tubular-like elements in microbodies have been reported in the testate amoeba *Trinema lineare* (Hedley & Ogden, 1974a), and in various Foraminifera by Hedley & Wakefield (in Hruban & Rechcigl, 1969) and Febvre-Chevalier (1971). Lattice-like structures within microbodies have been previously described in the Foraminifera *Shepheardella taeniformis* and *Globigerina bulloides* by Hedley *et al.* (1967) and Febvre-Chevalier (1971).

PSEUDOPODIA

In recent classifications (Loeblich & Tappan, 1961; Honigberg *et al.*, 1964) the class Rhizopodea has been divided – using the form of the pseudopodia as the distinguishing character – into three subclasses; the Lobosia, Filosia and Granuloreticulosa. In both classifications the superfamily Cryptodifflugiacea is included in the sub-class Lobosia. Previous studies (Penard, 1902; Page, 1966) demonstrate that the pseudopodia of *C. oviformis* appear to be intermediate in form between lobose and filose structures. Recognizing this difficulty, Deflandre (1953) erected a new sub-order the Reticulolobosa, but this has not been adopted in subsequent classifications.

In actively moving specimens of *C. oviformis* the pseudopodia are numerous, relatively long and appear to taper and have small branches. All these features are normally associated with filose pseudopodia (Pl. 5, fig. A).

Micrographs of whole animals which had been found with the pseudopodia extended (Pl. 5, fig. C) indicate that in addition to the main filose pseudopodia as seen with optical microscopy there are numerous ultrastructural pseudopodia or pseudopodial strands. These may or may not be connected to form a reticulum. These ultrastructural pseudopodia are similar to those seen in the granuloreticulose pseudopodia described for various foraminiferans by Hedley *et al.* (1967), Marszalek (1969) and Lengsfeld (1969).

Each pseudopodium appears to consist of ground-plasm, limited by a unit membrane, often containing bands of thick microfilaments and small electron-dense concentrations (Pl. 5, fig. B). In addition, some sections of pseudopodia contain strands of endoplasmic reticulum, Golgi bodies, membrane-bound vesicles and mitochondria, some of which may contain electron-dense calcium inclusions. The bands of thick microfilaments vary from 25 to 33 nm in diameter and are about 0·4 µm long (Pl. 5, fig. B). Microfilaments are sometimes found concentrated to form adhesion plaques at points of contact between opposing pseudopodia (Pl. 5, fig. D). We suggest that this reaction is probably restricted to contact between pseudopodia from different animals. Similar adhesion plaques have been reported in species of *Euglypha* by Hedley & Ogden (1973, 1974b).

The fine structure of the pseudopodia of *C. oviformis* is similar to that reported for other testate amoebae (Wohlman & Allen, 1968; Griffin, 1972; Eckert & McGee-Russell, 1973; Hedley & Ogden, 1973, 1974a) and naked amoebae (Comly, 1973; Taylor *et al.*, 1973; Rinaldi & Hrebenda, 1975) in having microfilaments as a structural element. Wohlman & Allen (1968) and Eckert & McGee-Russell (1973) suggest that both thin and thick microfilaments are associated with pseudopodia extension and contraction in *Difflugia*, and similar studies on slime moulds and naked amoebae by Komnick *et al.* (1972, 1973) suggest that the uptake and release of calcium ions by microfilaments plays an important role in cytoplasmic streaming. Another role for both types of microfilaments, that of cellular wound healing, has recently been suggested by Jeon & Jeon (1975) from studies on *Amoeba proteus*.

REPRODUCTION

The length of time required to double the population (doubling time) was estimated from three identical cultures established and maintained under similar conditions. Growth curves produced from observations made at regular intervals showed that the doubling time is between 29 and 41 hours.

The formation of a daughter cell by binary fission begins with an elongation of the cytoplasm of the parent shell to form a thick trunk which emerges from the aperture (Fig. 3·1). This trunk expands until the cytoplasm has reached about half the size of the parent shell. There is then a slight contraction, followed by further expansion until it reaches a size equivalent to that of the parent shell. At about this time the first indication of the transfer of cytoplasmic organelles becomes apparent, with the rapid passage of the dense granules into the daughter. The parent cytoplasm contracts slightly and is less active for a period of approximately 1 minute. The daughter then collapses slightly and the granules return to the parent. The rapid movement of the granules between the parent and daughter is repeated, and finally most of the granules are passed into the daughter with only one or two remaining in the parent (Fig. 3·6). The cytoplasm in the parent is reduced, to about one-third its normal volume and is situated at the aboral region of the shell, whilst the daughter cell appears to have reached full size. The connection between the two animals is reduced to a thin thread (Fig. 3·8). As the parental cytoplasm moves towards the apertural region of the shell, the connection between the parent and daughter is severed. Pseudopodia emerge from the parent and the two animals separate, the daughter remaining quiescent for periods in excess of 45 minutes from the time of separation.

The process of granular exchange takes place between 15 and 25 minutes after the first stages of division. Contractile vacuoles appear in the daughter after about 20 minutes, and the nuclei appear in both animals after about 30–35 minutes.

Often animals appear to start dividing only to cease at various stages, including stages that are almost half the parental size. These abortive products are rejected

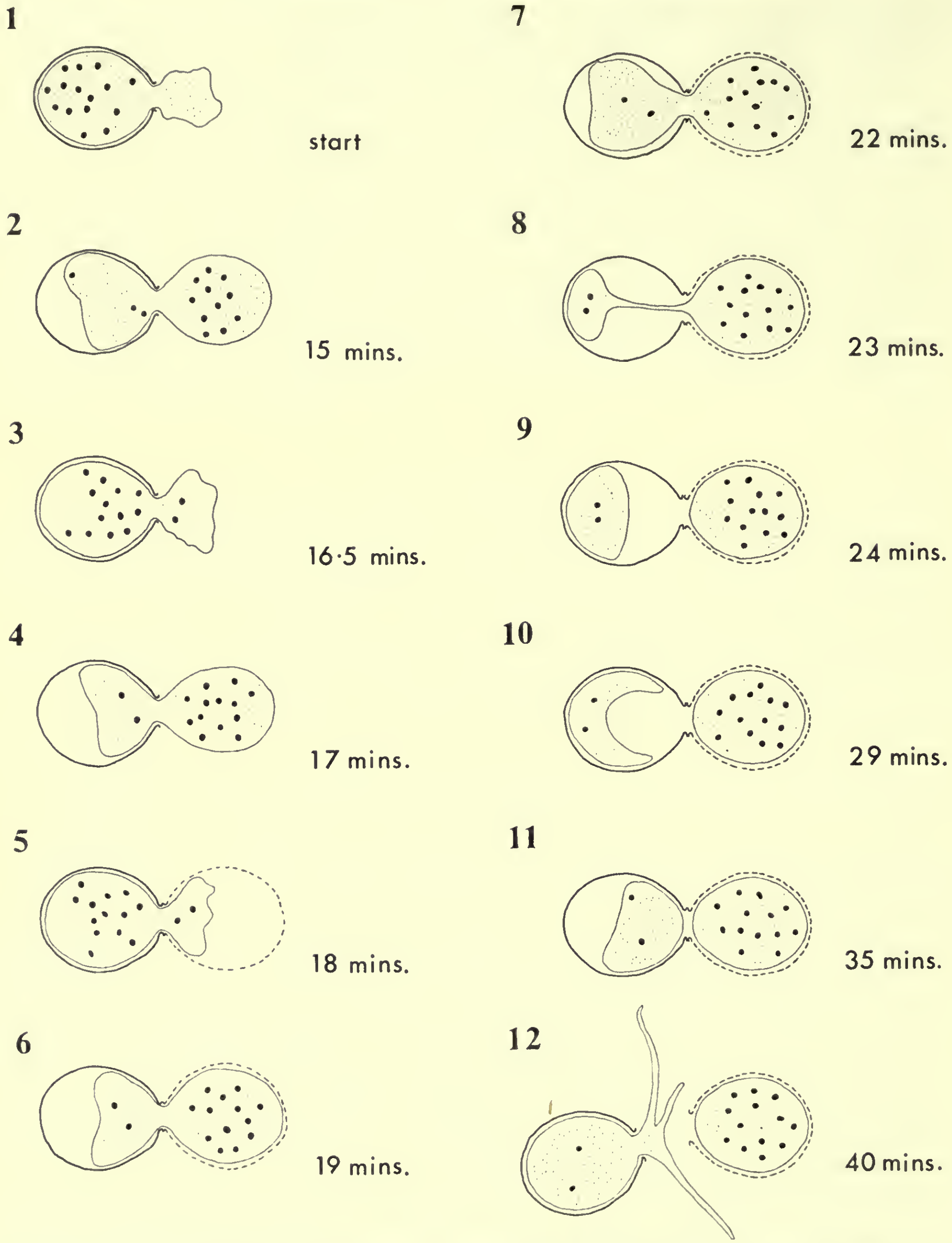
1
start
2
15 mins.
3
16·5 mins.
4
17 mins.
5
18 mins.
6
19 mins.
7
22 mins.
8
23 mins.
9
24 mins.
10
29 mins.
11
35 mins.
12
40 mins.

Fig. 3. Diagram showing the progressive stages in the formation of a daughter cell. At stage 1 the animal appears to rest for up to 15 minutes. Stages 2–7 represent the cytoplasmic contractions and rapid interchange of dense granules between the parent and daughter. Stage 5 shows the first indication of a thin shell (pecked line) surrounding the daughter, although this is probably present at an earlier stage. By stage 9 the cytoplasm has been divided between the parent and daughter and at stage 12 the parent moves away.

by the parent to become isolated, rounded lumps of cytoplasm, which are often seen in the cultures.

The first indication of a shell surrounding the newly formed daughter cell is a thin organic layer, indications of which are first seen after the start of granular exchange between parent and daughter. Nevertheless, it is possible that this organic layer is present around the initial extrusion of cytoplasm at the beginning of division. The formation of the shell in *C. oviformis* is probably dependent on the accumulation within the parent of reservoirs of an acid mucopolysaccharide and calcium ions. The organic material we believe is produced by both the Golgi complexes and the dense endoplasmic reticulum, and is stored in the cytoplasm at the storage areas (Pl. 3, fig. A ; Pl. 4, fig. B). The fusion of vesicles to form storage areas appears to represent a process of intake and assimilation. There is no evidence to suggest how this material is distributed from this reservoir, but the storage areas are absent in young daughter cells. A similar aggregation of vesicles rich in polysaccharides has been demonstrated by Holtrop (1972) in cartilage cells of the epiphyseal plate, where the protein polysaccharide complex was considered to assemble before it was extruded into the matrix.

Calcification of the shell appears to start shortly after division. During the early stages of calcification the shells often have an irregular outline (Pl. 6, fig. B), and they appear to be flexible. This initial shell wall has a diffuse appearance, with some small concentrations of electron-dense material on the inner surface (Pl. 5, fig. E). When the parent and daughter cells have finally divided they separate and the aperture of the daughter is sealed by a thin, fibrous organic membrane (Pl. 6, fig. A). In the cytoplasm of the daughter cell the usual membrane-limited profiles of endoplasmic reticulum are absent and it appears to be a mass of free ribosomes. The small circles of ribosomes that are seen (Pl. 5, fig. E) are possibly the initial stages in the reformation of these profiles.

In *C. oviformis* it has been possible to locate only one site where calcium is concentrated. This is between the outer and inner mitochondrial membranes where it is stored as spherical inclusions of amorphous calcium phosphate (Pl. 3, fig. B). Most of these mitochondria pass at division into the daughter cell. Several young animals examined shortly after division contain mitochondria without inclusions and in such cases the matrix of the mitochondria appears to be homogeneous, the cristae are not readily resolved, and the outer mitochondrial membrane is seen to have small swellings (Pl. 5, fig. F). It has been established by Wasserman & Kallfelz (1970) that calcium ions are actively transported across mitochondrial membranes, and a model for this transport has been proposed by Rasmussen (1966). Previous investigations (Greenawalt *et al.*, 1964 ; Greenawalt & Carafoli, 1966 ; Thomas & Greenawalt, 1968) on calcium-rich granules in mitochondria suggest that formation takes place in three stages. First at the inner membrane surfaces, especially on the cristae, followed by free granules in the matrix and finally the granules grow by accumulation.

Opinions differ over the factors that induce concentrations of calcium in the mitochondria of the ciliated protozoan *Spirostomum ambiguum*, where they have been considered to be a mobile endoskeleton (Bien, 1967), a metabolic store of phosphate (Pautard, 1970), or concentrations of waste calcium (Jones, 1967, 1969). But in vertebrates it has been suggested that similar mitochondrial inclusions to those demonstrated here in *C. oviformis* are involved in mineralization of deer antlers (Sayegh *et al.*, 1974) and eggshell formation in chickens (Hohman & Schraer, 1966).

CYST

After 4 or 5 weeks encysted animals appear in cultures. Such animals have a distinct operculum forming a seal across the aperture (Pl. 6, fig. E) and the ultrastructure of this operculum is a finely fibrillar matrix interspersed with small naturally electron-dense bodies (Pl. 6, fig. D). Results from periodic acid-Schiff tests carried out by Page (1966) suggest that the operculum is mainly of a polysaccharide nature.

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PLATE 1

Cryptodifflugia oviformis

FIG. A. Specimen to illustrate the circular aperture and the apertural collar (arrowed). × 2500

FIG. B. Section showing one side of the apertural collar. Note that the calcareous layer continues as a border (arrow) to the organic collar (oc). × 30 100

FIG. C. Section through the aperture of a specimen treated with EDTA to remove the calcareous layer. Note the thin organic layer (ol) and thickened collar (oc). × 5800

FIG. D. Section through aperture of specimen treated with EDTA, to show the extension of the organic layer (ol) to form the collar. × 27 000

FIG. E. Section of shell wall stained with thiosemicarbazide/silver proteinate, showing silver deposited at the organic layer (ol). The gap (g) represents the calcareous layer removed during the staining technique. × 24 000

FIG. F. Abnormal shell showing irregular patterning of the shell and two apertural openings (arrowed). × 1600

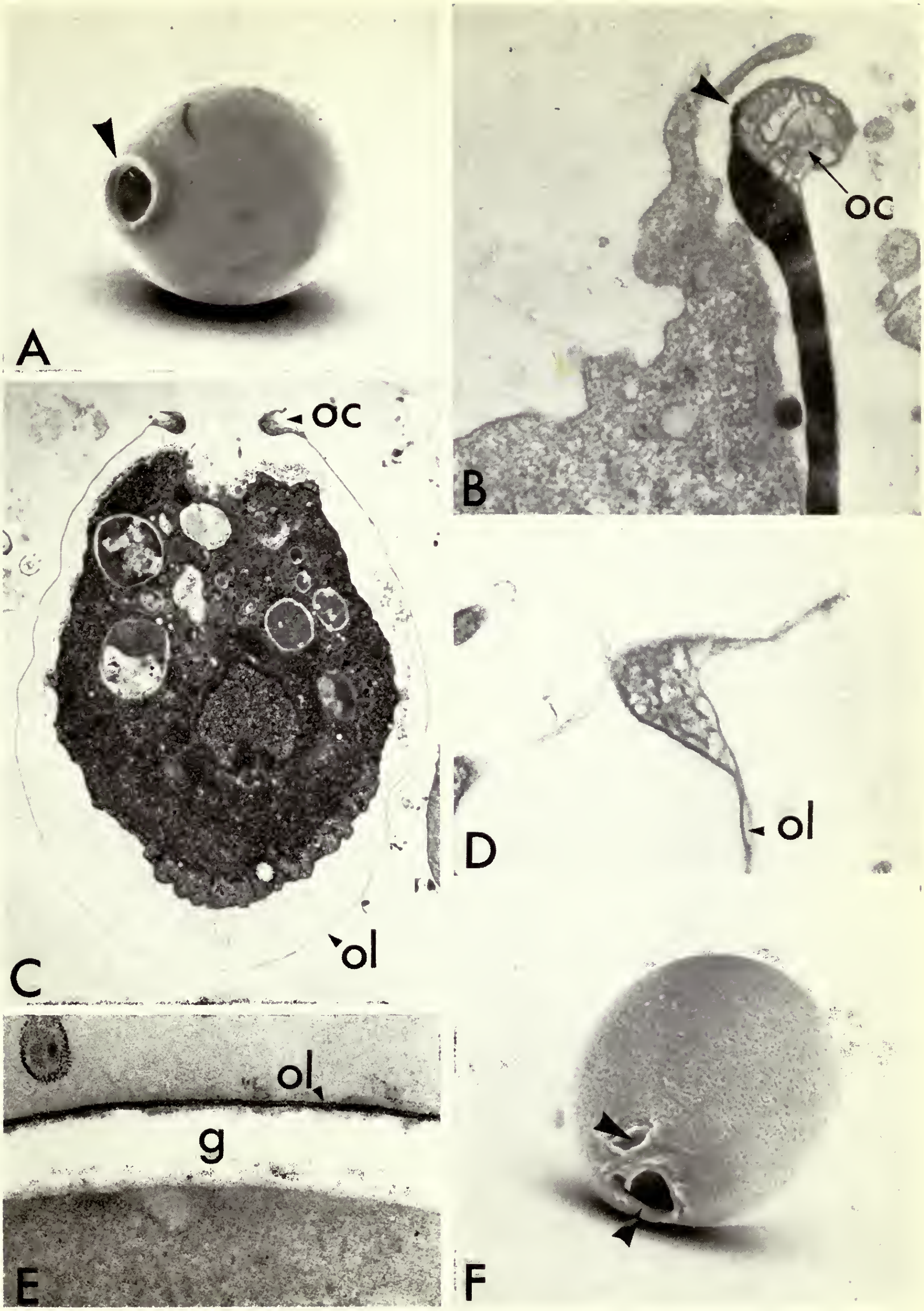

A
oc
B
oc
C
ol
ol
D
ol
g
E
F

PLATE 2

Cryptodifflugia oviformis

Section through the aperture of a whole specimen to show the nucleus (n), Golgi bodies (G), granular endoplasmic reticulum (ger) and food vacuoles (fv). × 8600

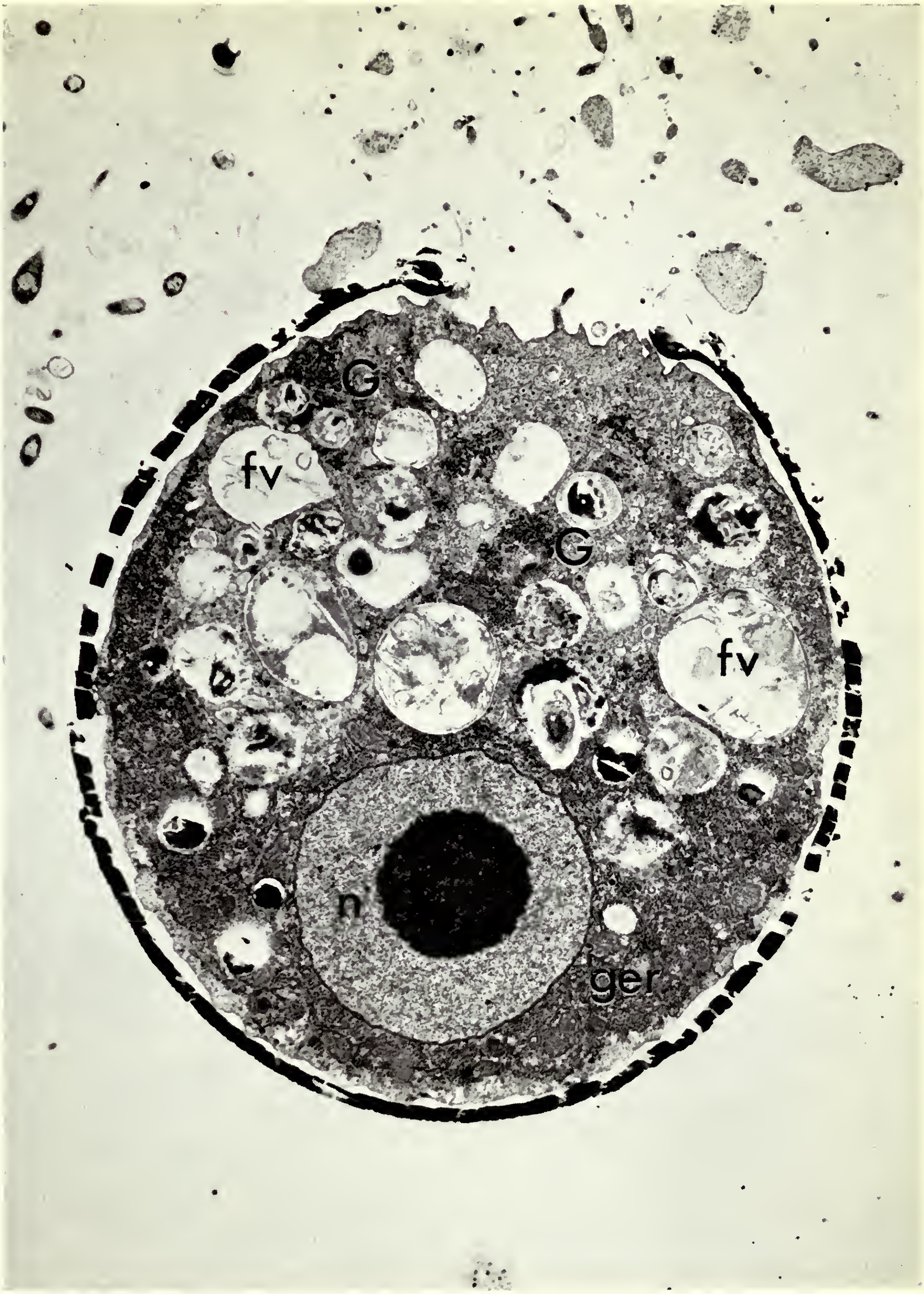

G
fv
G
fv
n
ger

PLATE 3

Cryptodifflugia oviformis

Fig. A. Section to show the nucleus (n), contractile vacuoles (cv), storage area (sa) and mitochondria containing calcareous inclusions (mc). × 7800

Fig. B. Section of a mitochondrion (m) with a calcareous inclusion. × 15 600

Fig. C. Section through a Golgi body to illustrate the formation of vesicles with electron-dense contents at the margin of the saccules (arrowed). × 44 600

Fig. D. Section showing membrane-bound vesicles (mbv) with a thin electron-dense lining and an electron-lucent centre. × 44 600

Fig. E. Two Golgi bodies (G) in a region of dense endoplasmic reticulum. Note the presence of membrane-bound vesicles (mbv) at the inner face of the saccules. × 30 100

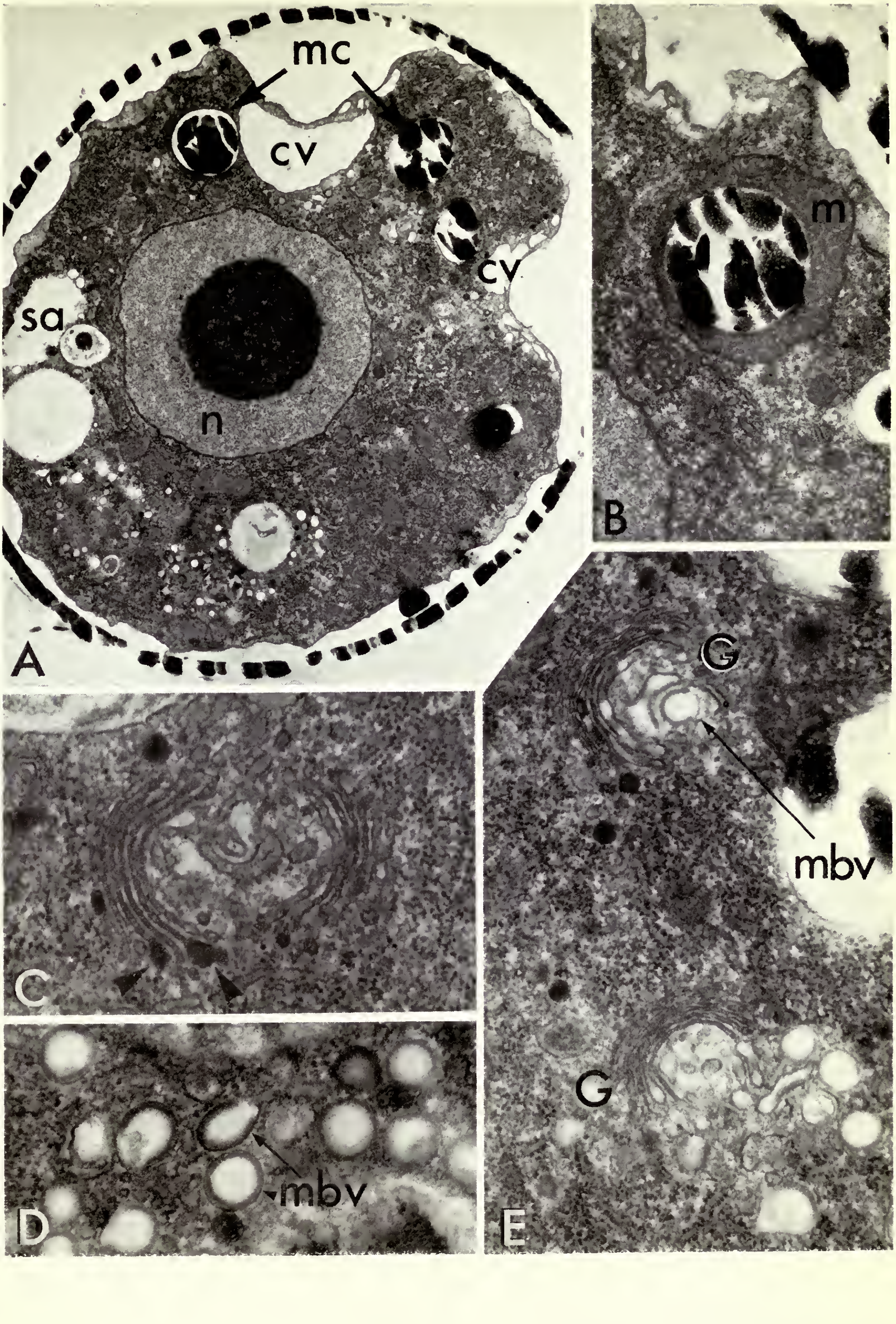

mc
cv
cv
sa
n
A
m
B
G
mbv
C
mbv
D
G
E

PLATE 4

Cryptodifflugia oviformis

FIG. A. Section to illustrate a large electron-lucent vesicle (lv) and the associated band of endoplasmic reticulum (er). × 11 500

FIG. B. Section stained with thiosemicarbazide/silver proteinate, showing silver deposited at the storage areas (sa), Golgi bodies (G) and the membrane-bound vesicles (mbv). × 10 000

FIG. C. Transverse section showing the position of the storage areas (sa), food vacuole (fv), contractile vacuoles (cv) and nucleus (n). × 7800

FIG. D. A typical storage area showing three types of vesicles, electron-dense (ed), membrane-bound (mbv) and large vesicles (lv). Note that the large vesicles contain an electron-dense material. × 13 500

FIG. E. Section through a microbody with tubular elements. × 75 600

FIG. F. Section through a microbody containing a lattice-like structure. × 90 600

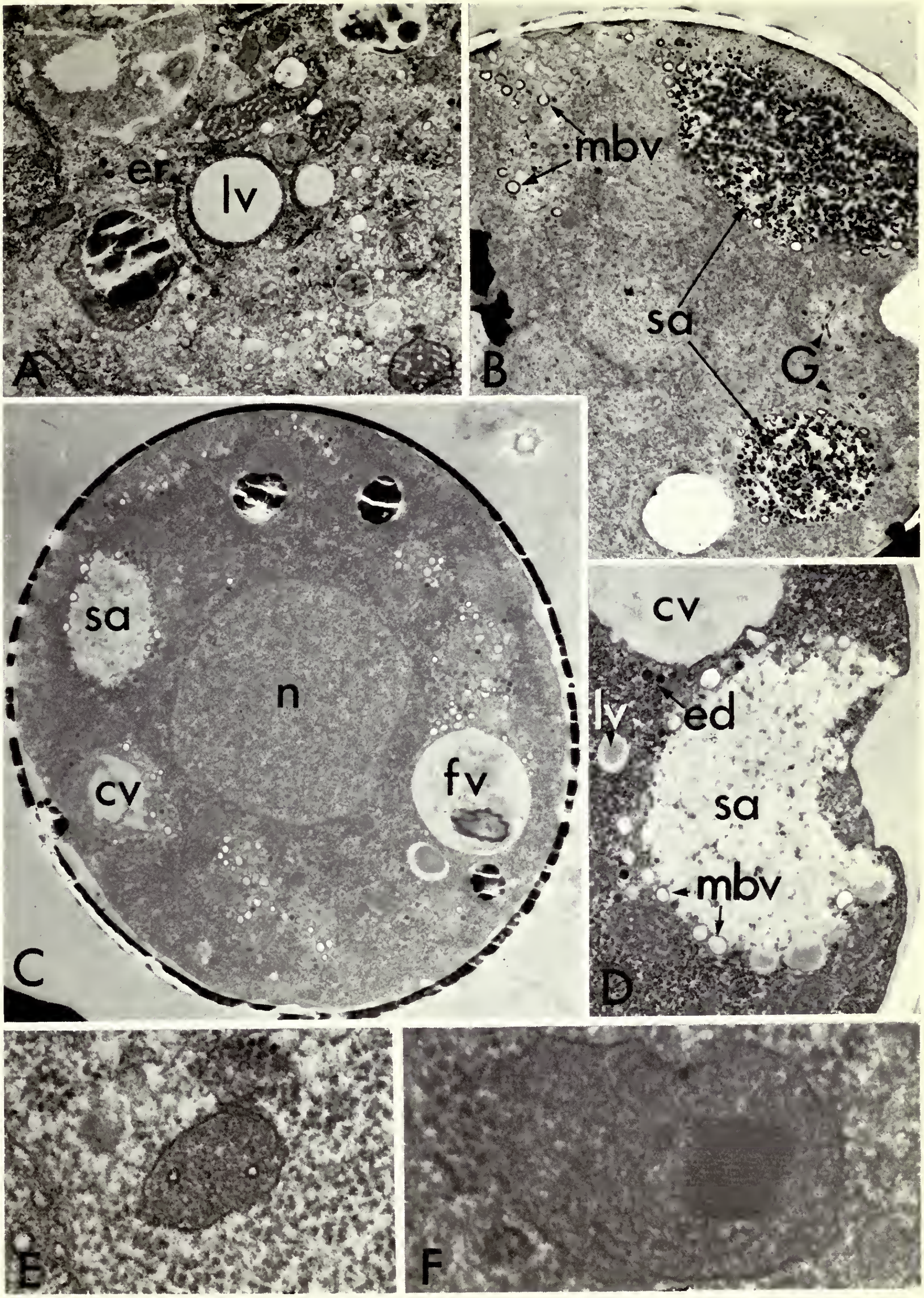

er
lv
A
mbv
sa
G
B
sa
n
cv
fv
C
cv
ed
lv
sa
mbv
D
E
F

PLATE 5

Cryptodifflugia oviformis

Fig. A. Specimen on an agar surface to illustrate the pseudopodia extended. ×960

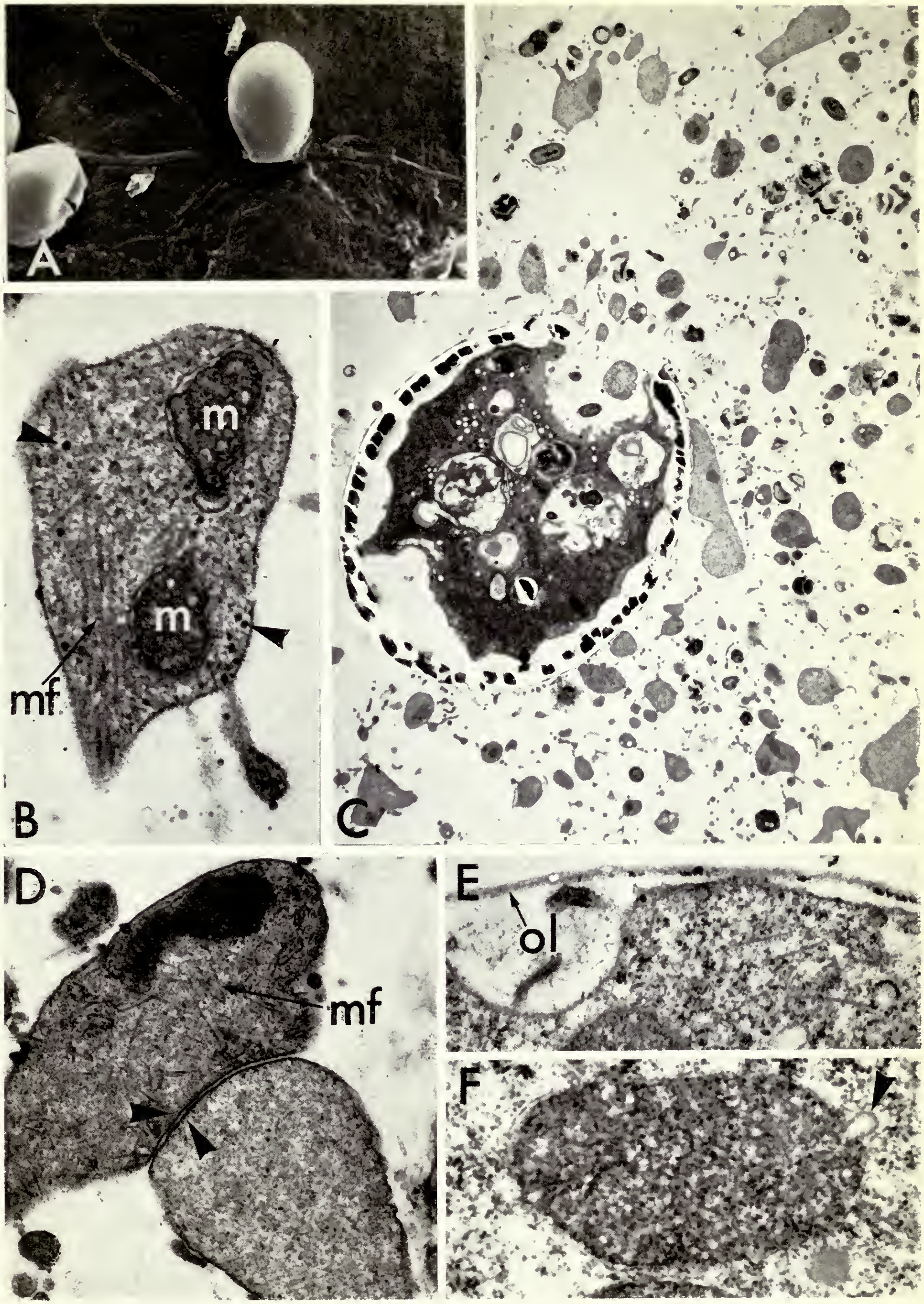
Fig. B. Section through a pseudopodium containing mitochondria (m), bundles of microfilaments (mf) and small electron-dense concentrations (arrowed). ×44 600

Fig. C. Section of a specimen to illustrate the range and abundance of pseudopodia. ×4300

Fig. D. Section through two pseudopodia showing that the opposed membranes are parallel in the region of contact. Note the thickening of those membranes (arrowed) and the bundles of microfilaments (mf). ×15 000

Fig. E. Section of partially calcified daughter cell, showing the organic layer (ol) with small concentrations of electron-dense material at the inner surface. ×20 100

Fig. F. Section of a mitochondrian with a homogeneous matrix and apparent absence of cristae. A swelling of the membrane is arrowed. ×30 100


A
m
m
mf
B
C
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mf
E
ol
F

PLATE 6

Cryptodifflugia oviformis

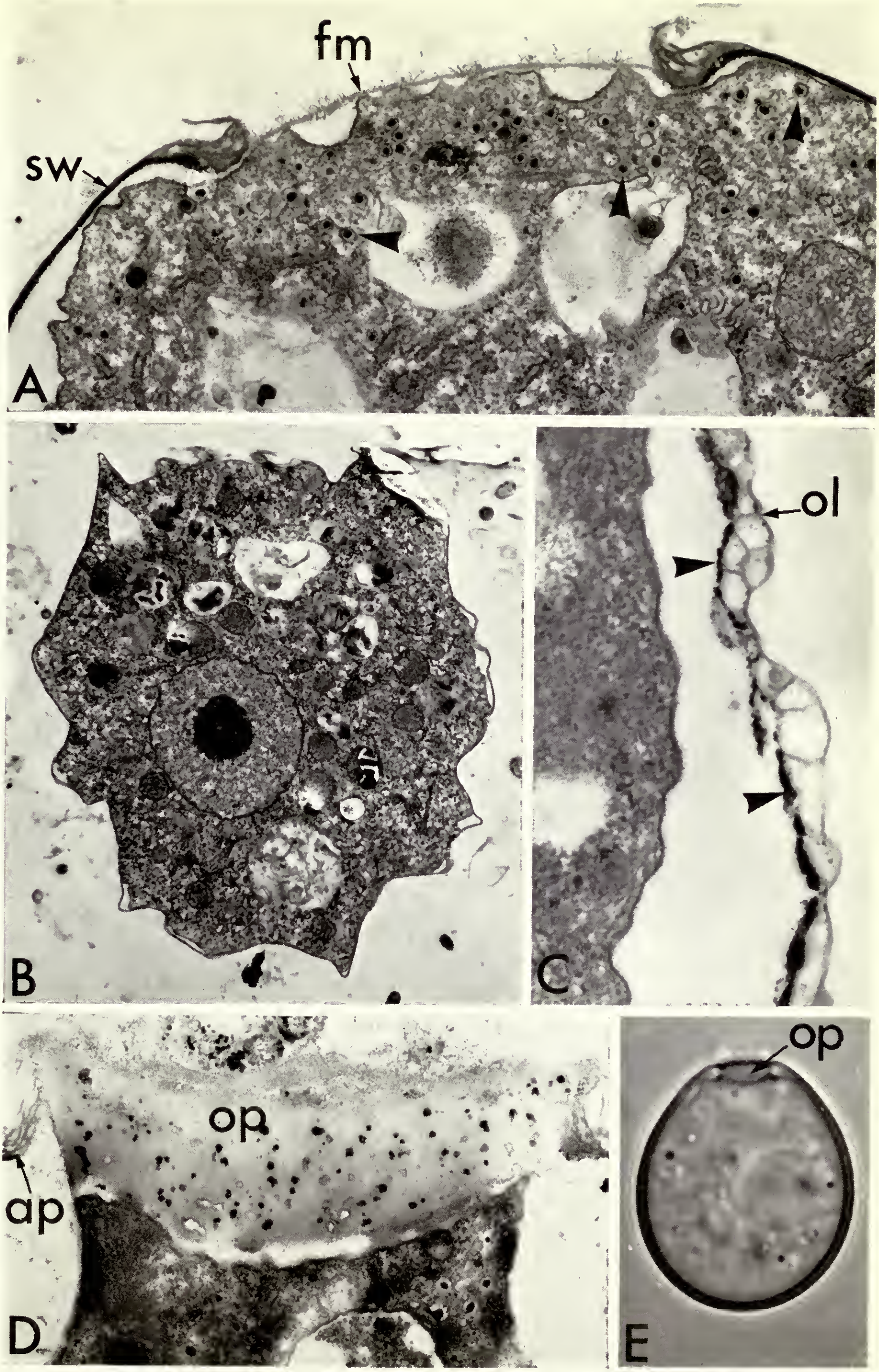
Fig. A. Section through the aperture of a partially calcified daughter cell. Note the thin shell wall (sw), the band of fibrillar organic material (fm) sealing the aperture and the vesicles containing electron-dense material (arrowed). × 20 100

Fig. B. Section of a young daughter cell illustrating the irregular outline of the uncalcified shell. × 5800

Fig. C. Section of shell wall of abnormal specimen. Note the folded organic layer (ol) and the small concentrations of calcified material on the inner surface (arrowed). × 30 100

Fig. D. Section through an aperture (ap) sealed with an operculum (op). × 28 400

Fig. E. Light micrograph showing the operculum (op) in the apertural opening. × 2000


fm
sw
A
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op
E

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THE LARVAL AND POST-LARVAL DEVELOPMENT OF THE SCORPION SPIDER CRAB, *INACHUS DORSETTENSIS* (PENNANT) (FAMILY: MAJIDAE), REARED IN THE LABORATORY

R. W. INGLE

BULLETIN OF
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Pp. 329–348 ; 10 *Text-figures*

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THE LARVAL AND POST-LARVAL DEVELOPMENT OF THE SCORPION SPIDER CRAB, *INACHUS DORSETTENSIS* (PENNANT) (FAMILY : MAJIDAE), REARED IN THE LABORATORY

By R. W. INGLE

INTRODUCTION

The Scorpion Spider Crab, *Inachus dorsettensis* (Pennant), occurs from Norway, through the north Atlantic to the Mediterranean and along the west and South African coasts as far as Natal, being confined to littoral waters to depths of 550 m (Monod, 1956 : 529). It is reported from hard to muddy substrates (Christiansen, 1969 : 102) although in British waters it has been taken chiefly in areas of sandy-mud (Marine Biological Association, 1957 : 260 ; Hartnoll, 1963 : 434). In British waters this species breeds throughout the year (Lebour, 1928 : 502).

Although adults of the three British *Inachus* species are readily distinguishable from each other, the larval and post-larval stages cannot be reliably identified at present because of the lack of adequate descriptions. Recently *I. dorsettensis* was reared to ninth crab stage in the laboratory and the early developmental stages are described in detail below.

MATERIAL AND METHODS

Larvae were hatched from crabs collected on or near the Eddystone Grounds, off Plymouth, Devonshire, England, and were reared using the method described by Rice & Ingle (1975 : 104).

Larvae and moults were preserved in 70% alcohol and in 5% buffered formal-saline. Dissections were made in polyvinyl-lactophenol/lignin pink medium. Drawings and measurements were made with the aid of a *camera lucida*. The measurements taken were : dorsal spine length (*D.S.*) = distance between tip of dorsal spine and rostrum, and carapace length (*C.L.*) = distance between base of eyestalk and posterio-lateral margin of carapace. Between 5 and 10 suitable specimens of each stage were measured. Sizes given under Dimensions are those for the smallest and the largest specimens.

RESULTS

Most females hatched their total brood within a period of 36 hours ; a few took up to 48 hours. All successfully reared larvae hatched as free-swimming zoeae. The small percentage that hatched as pre-zoeae all died within 24 hours.

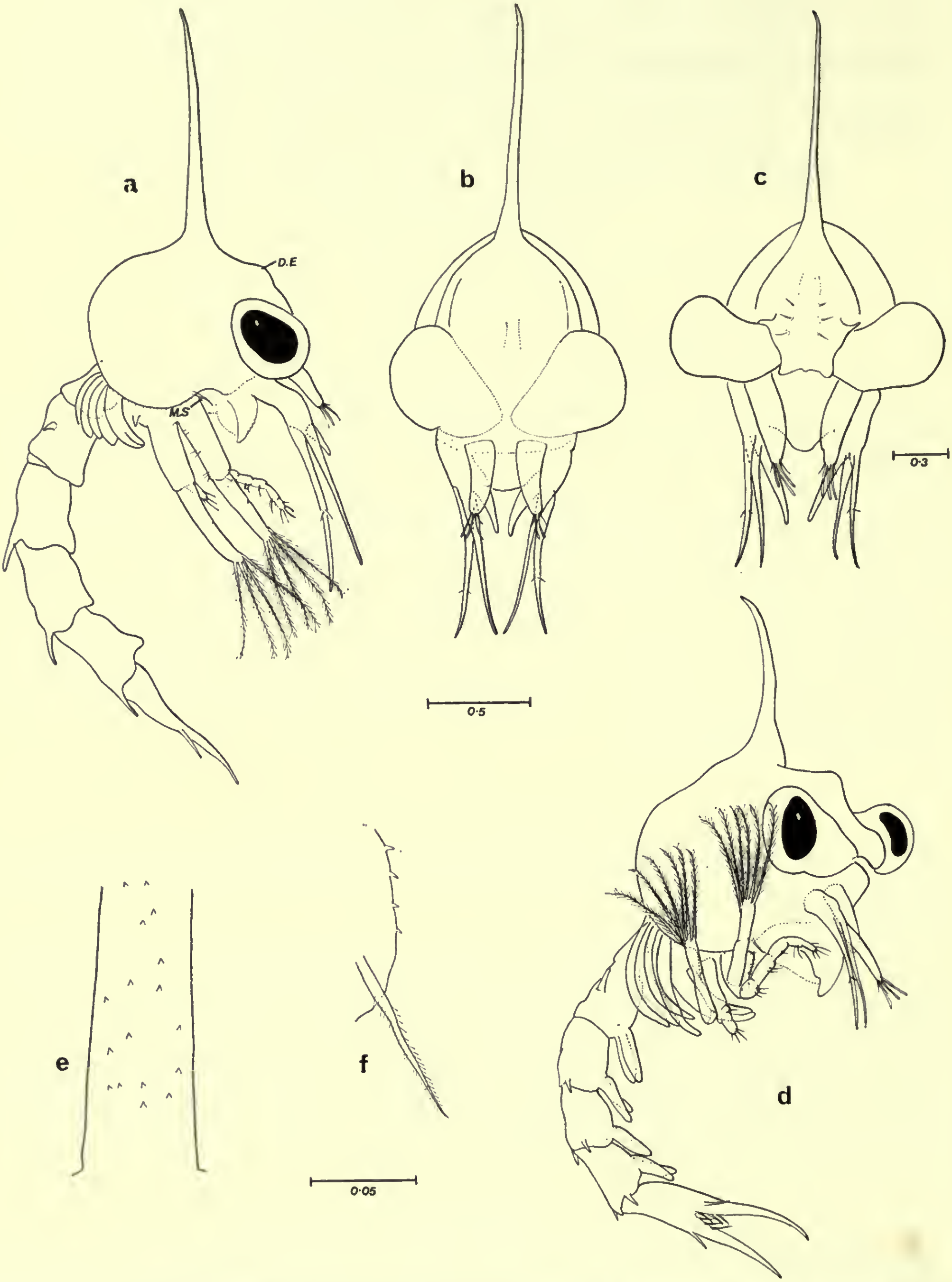

FIG. 1. *Inachus dorsettensis*, lateral and frontal aspects of zoeal stages: (a), (b) first zoea and (c), (d) second zoea; (e) basal part of dorsal spine of first zoea; (f) majid spine of first zoea. Scales in millimetres.

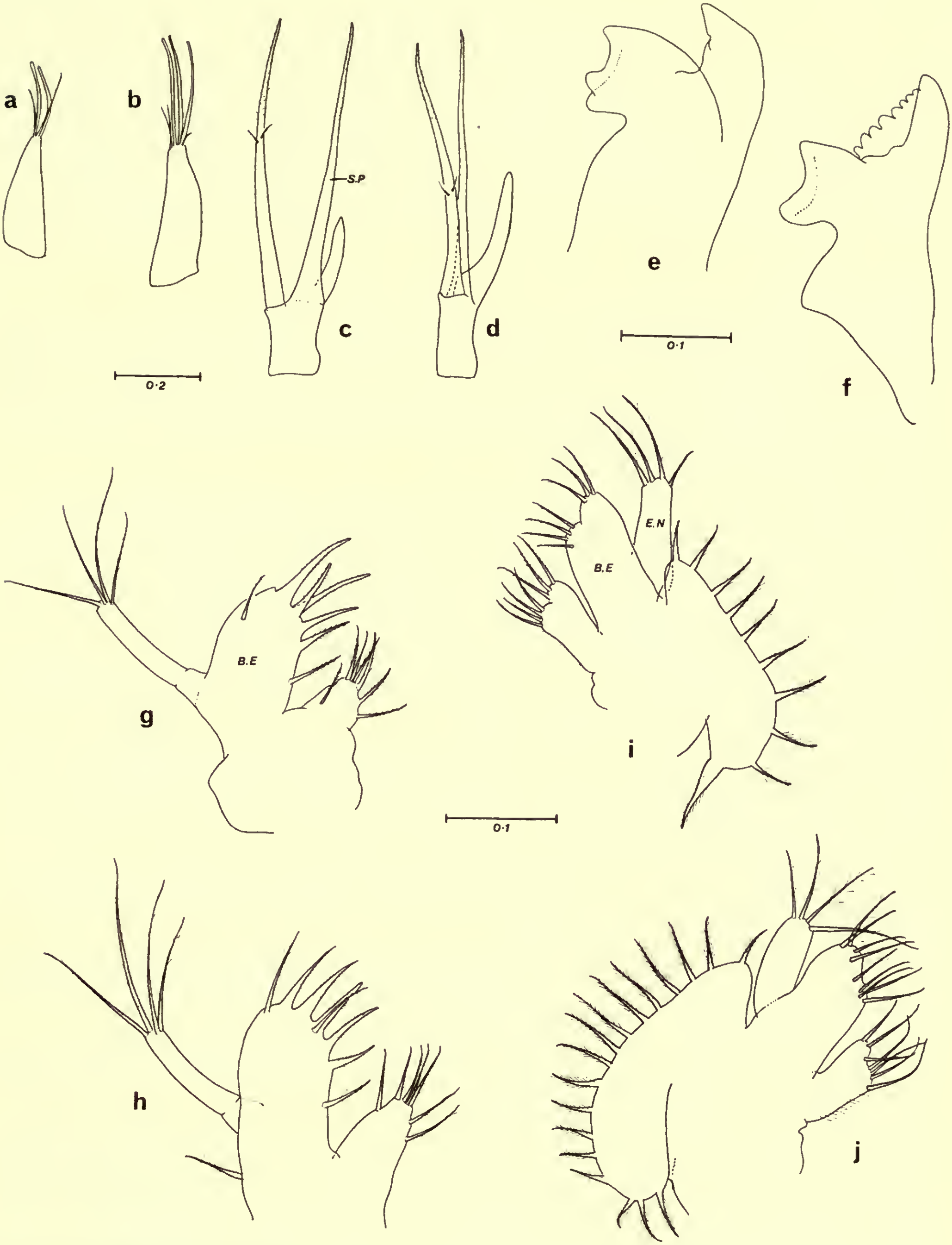
a
b
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FIG. 2. *Inachus dorsettensis*, (a), (b) antennule; (c), (d) antenna; (e), (f) mandible; (g), (h) maxillule; (i), (j) maxilla of: (a), (c), (e), (g), (i) first zoea and (b), (d), (f), (h), (j) second zoea. Scales in millimetres.

DESCRIPTIONS

Inachus dorsettensis (Pennant)

Larval references. *Inachus scorpio* Claus, 1876 : Taf. X, fig. 8 (1st zoea) ; non *Inachus scorpio* Cano, 1893 : Taf. 35, fig. 7 (1st zoea) = *I. thoracicus* (Roux) ; *Inachus dorsettensis* Lebour, 1927 : 795 ; Pl. I, figs 1, 4–6 (pre-zoea), fig. 7 (1st zoea), Pl. II, figs 1, 4–7, Pl. IV, figs 1, 3 (2nd zoea), Pl. II, fig. 10, Pl. III, figs 1, 7, 8, Pl. IV, figs 2, 4 (megalopa), Pl. III, fig. 8 (1st–3rd crab) ; 1928 : 546, Pl. III, fig. 5 (1st zoea, col. fig.), Pl. XV, fig. 4 (1st crab), fig. 5 (2nd crab) ; Heegaard, 1963 : 471 (1st zoea), Pl. XVII (coloured fig.), text-figs 70–76.

First zoea

Dimensions : *D.S.* 1·9–2·0 mm ; *C.L.* 0·9–1·0 mm.

Carapace (Fig. 1a, b) : Dorsal spine well developed, apically curved, armed with minute spinules most numerous at base (Fig. 1e). Rostral and lateral spines absent. Dorso-median elevation (*D.E.*) prominent ; majid spine (*M.S.*) plumose, arising from inner ventral carapace margin and well developed (Fig. 1f), posterio-ventral margin of carapace spinulate.

Eyes : Partly fused to carapace.

Antennule (Fig. 2a) : Unsegmented with two terminal aesthetascs and 2 setae.

Antenna (Fig. 2c) : Spinous process (*S.P.*) about $\frac{2}{3}$ length of dorsal spine, distal $\frac{1}{3}$ invested with minute spinules. Exopod as long as spinous process with 2 median spines, distal $\frac{1}{3}$ spinulate. Endopod about $\frac{1}{3}$ length of spinous process.

Mandible (Fig. 2e) : Incisor and molar process developed, palp absent.

Maxillule (Fig. 2g) : Endopod 2-segmented, distal segment about 4× length of proximal and with 4 distal setae ; basal endite (*B.E.*) with 5 setosed spines and 2 setae, coxal endite with 7 plumose setae.

Maxilla (Fig. 2i) : Endopod (*E.N.*) narrow, apex truncate with 3 long and 1 (outermost) short plumose setae ; basal endite (*B.E.*) bilobed with 7–8 plumose setae ; coxal endite bilobed with 7 plumose setae, inner margin invested with fine setules. Scaphognathite with 10 plumose setae, distal one very stout, posterior lobe short.

First maxilliped (Fig. 3a) : Basis with 9 setae (arranged 2, 2, 2, 3), endopod 5-segmented with 3, 2, 1, 2, 4 + 1 setae respectively ; exopod incipiently 2-segmented, distally with 4 terminal plumose setae.

Second maxilliped (Fig. 3b) : Basis devoid of setae, endopod 3-segmented with 0, 1, 3 + 1 setae respectively, distal segment about 3× length of proximal, exopod incipiently segmented, distally with 4 plumose setae.

Third maxilliped (Fig. 3c, MX) : Represented as a small unsegmented bud.

Peraeopods (Fig. 3c) : Conspicuous, 1st incipiently chelate, 2nd–5th unsegmented as terminally acute finger-like projections.

Abdomen (Fig. 4a, b) : 5-segmented + telson. Segments 2–5 with incipient pleopod buds ; 2nd segment with pair of forwardly directed dorso-lateral processes, segments 3–5 each with a pair of long posterior dorso-lateral spines and with posterior ventro-lateral margins rounded to truncate. Posterio-dorsal margin of segments 2–5 each with a pair of small setae. Telson forks long, not diverging posteriorly, lateral spines (*L.S.*) long, nearly $\frac{1}{3}$ length of forks, both invested with minute spinules ; each half of telson posterior margin convex, with 3 plumose setae.

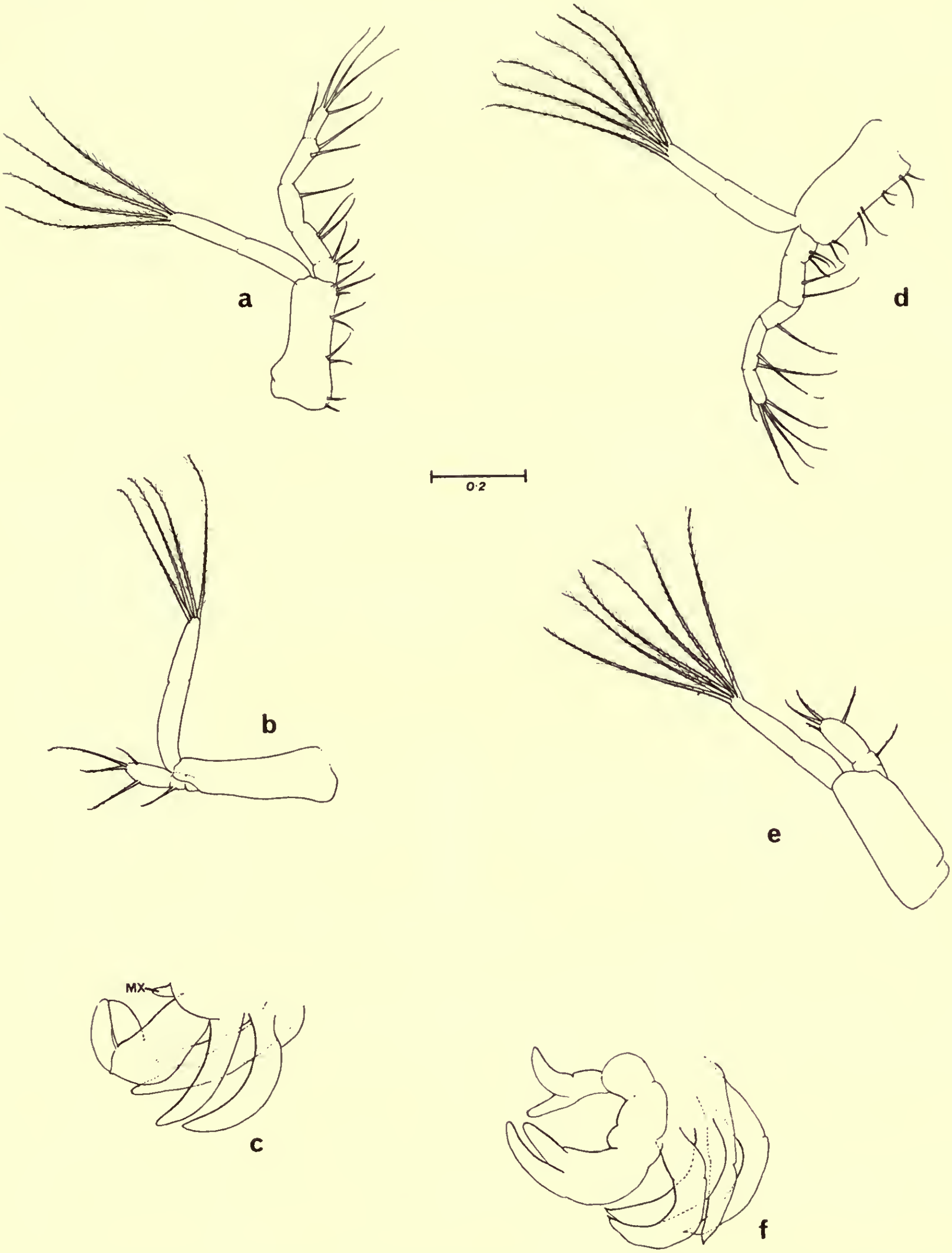

Fig. 3. *Inachus dorsettensis*, (a), (d) first maxilliped; (b), (e) second maxilliped; (c), (f) third maxilliped and peraeopods of: (a)–(c) first zoea and (d)–(f) second zoea. Scale in millimetres.

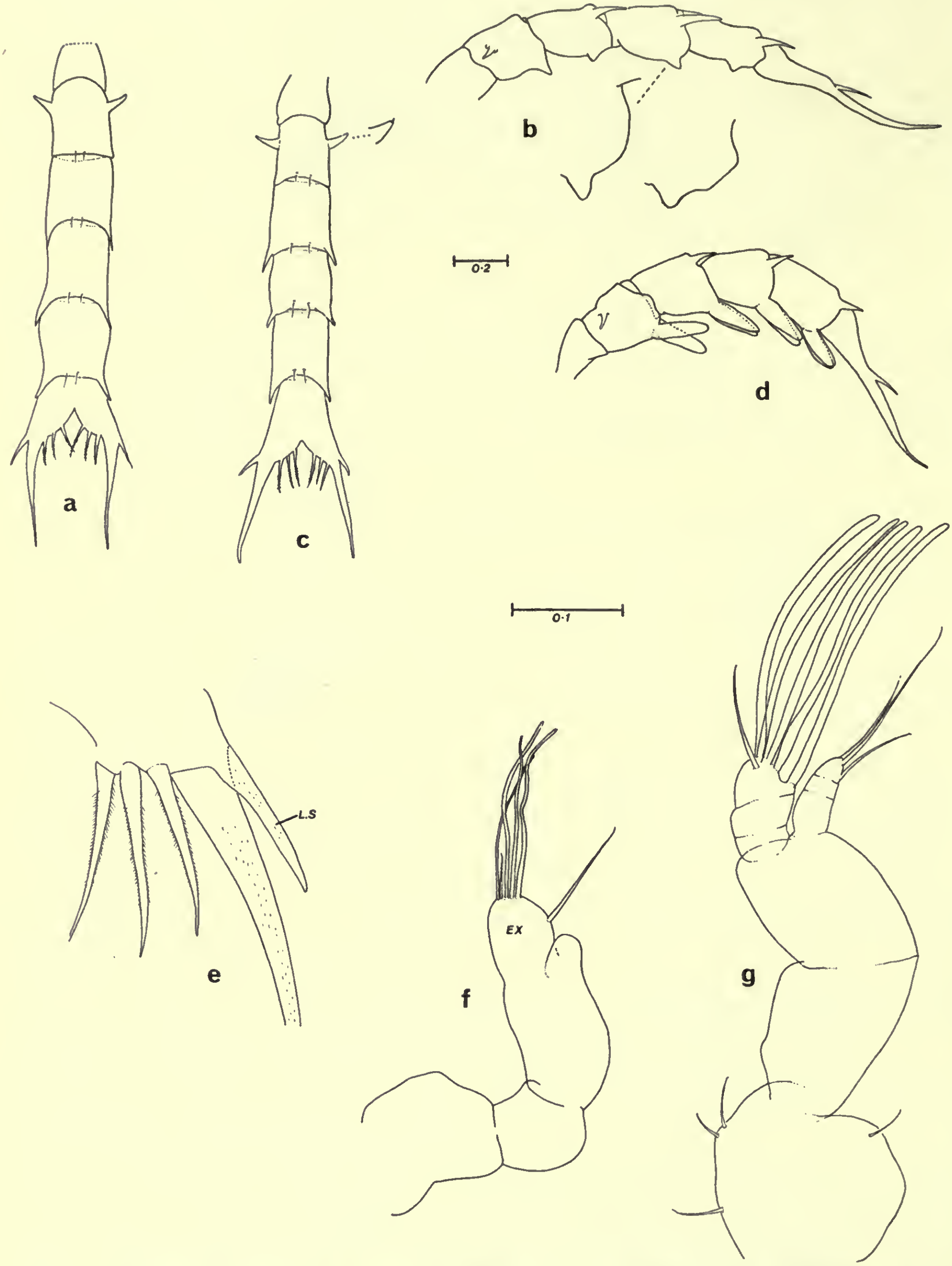

FIG. 4. *Inachus dorsettensis*, abdomen, dorsal (a), (c) and lateral (b), (d) aspects of (a), (b) first zoea and (c), (d) second zoea ; (e) right half of telson of second zoea ; (f) antennule of megalopa ; (g) antennule of first crab. Scales in millimetres.

SECOND ZOEA

Dimensions: *D.S.* 1·7–1·8 mm; *C.L.* 1·2–1·3 mm.

Carapace (Fig. 1c, d): Dorsal spine slightly more curved and shorter than in first stage, dorso-median elevation more pronounced and now with 2 rows of 3 setae; rostrum pronounced, ocular eaves developed.

Eyes: Now stalked.

Antennule (Fig. 2b): Now with 3 terminal aesthetascs and 3 setae.

Antenna (Fig. 2d): Endopod now about ½ length of spinous process.

Mandible (Fig. 2f): Distal margin of incisor process cut into rounded teeth.

Maxillule (Fig. 2h): Outer margin of basal endite now with a plumose seta, distal margin now with 3 setae.

Maxilla (Fig. 2j): Outermost plumose seta of endopod longer than in first stage; basal endite with 9 plumose setae; scaphognathite with 17 plumose setae, distal one no longer stout.

First maxilliped (Fig. 3d): Exopod now with 6 terminal plumose setae.

Second maxilliped (Fig. 3e): Exopod now with 6 terminal plumose setae.

Third maxilliped (Fig. 3f): Now a pronounced bilobed bud.

Peraeopods (Fig. 3f): 2nd–5th incipiently segmented.

Abdomen (Fig. 4c, d): Segments 2–5 with well-developed pleopod buds, dorso-lateral processes on 2nd segment longer than in first stage and with terminal spinules; posterior dorso-lateral spines shorter than in first stage; telson forks diverging posteriorly, spinules (Fig. 4e) conspicuous.

MEGALOPA

Dimensions: *C.L.* 1·1–1·2 mm.

Carapace (Fig. 10a): Longer than broad, narrowing anteriorly. Front with a pair of widely spaced anteriorly directed acute frontal horns and medially with an obtuse protuberance; protogastric region with 3 transverse low tubercules, outermost 2 spined; cardiac with 3 spines transversely placed, intestinal with a low posteriorly placed tubercule.

Eyes: Large and long, cornea well developed.

Antennule (Fig. 4f): Peduncle 3-segmented, exopod (*EX*) not demarcated from peduncle, with 4 aesthetascs and 2 setae, endopod vestigial.

Antenna (Fig. 5d): 6-segmented, flagellum not demarcated from peduncle. First segment with ventrally directed spine and outwardly directed obtuse process, 3rd segment with 1 seta, 5th segment longest with 4 terminal setae, 6th with 2 long and 1 short terminal setae.

Mandible (Fig. 5a): Incisor process well developed, molar reduced, now with 3-segmented mandibular palp, distal segment with 1–2 setae.

Maxillule (Fig. 5b): Endopod now reduced, unsegmented; basal endite with 6 spines and 5–7 setae, spines thinner than in zoeal stages.

Maxilla (Fig. 5c): Endopod reduced to terminally acute process; basal endite slightly bilobed with 9–10 plumose setae; coxal endite slightly bilobed with 5 plumose setae. Scaphognathite with 22 plumose setae shorter than in zoeal stages.

First maxilliped (Fig. 6a): Coxal endite (*C.E.*) bilobed, invested with 1 and 4 setae

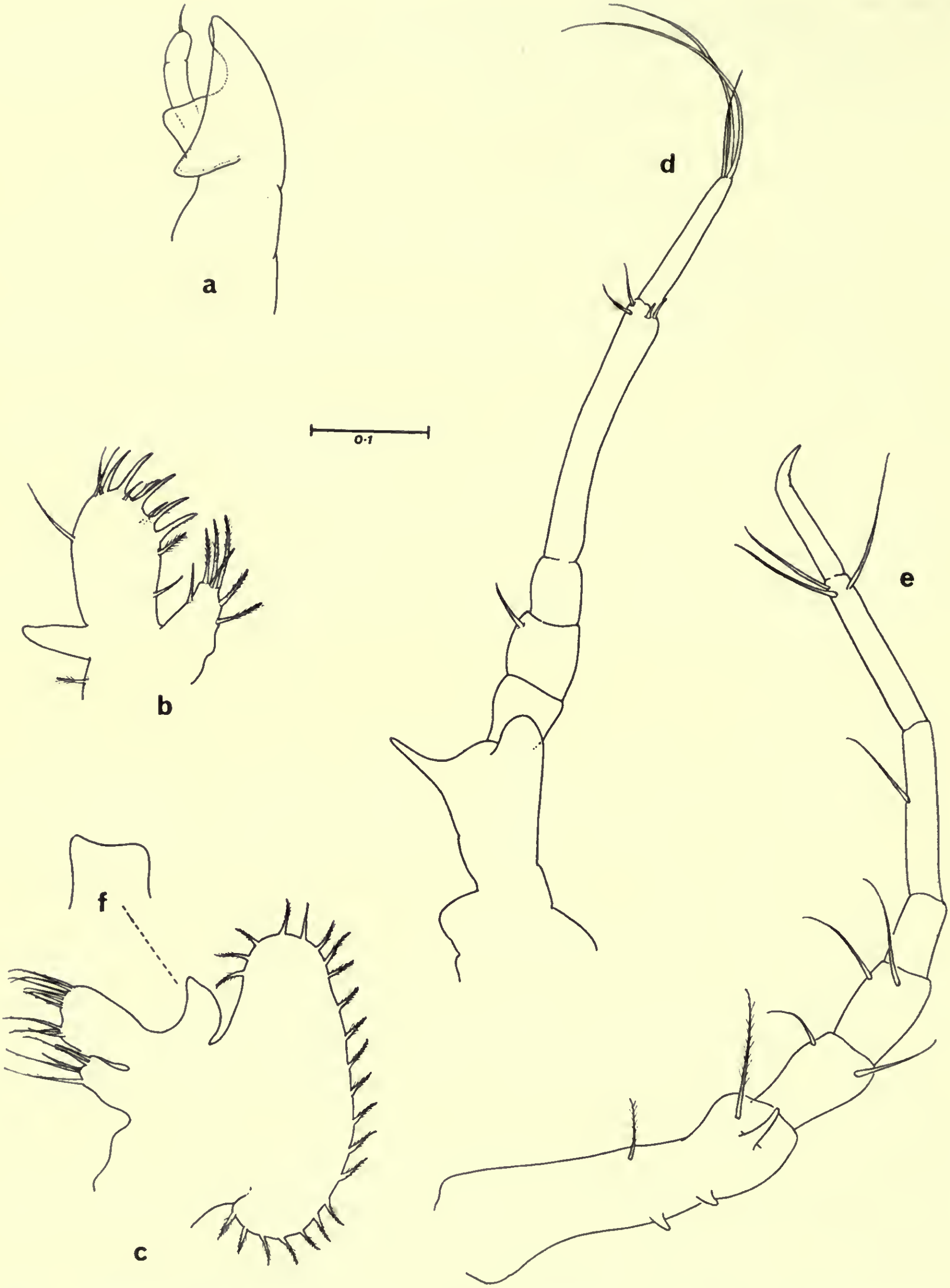

FIG. 5. *Inachus dorsettensis*, (a) mandible, (b) maxillule, (c) maxilla and (d) antenna of megalopa ; (e) antenna and (f) endopod of maxilla of first crab. Scale in millimetres.

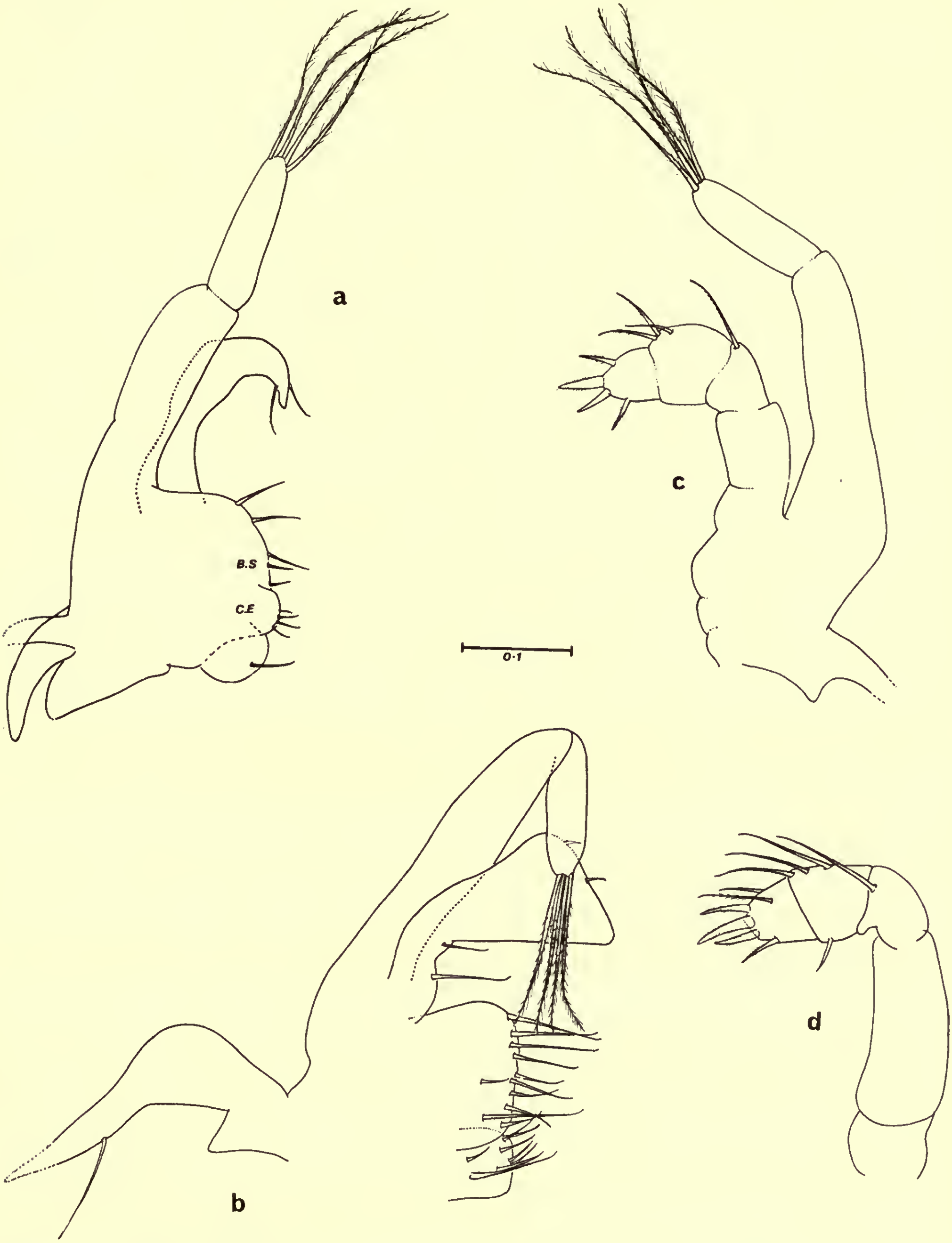

FIG. 6. *Inachus dorsettensis*, first maxilliped of (a) megalopa and (b) first crab ; second maxilliped (c) of megalopa and (d) endopod of second maxilliped of first crab. Scale in millimetres.

respectively ; inner margin of basis (*B.S.*) with 5 setae. Exopod long, stout, 2-segmented, distally with 4 long terminal plumose setae ; endopod curved with 1–2 subapical setae, epipod short, bilobed.

Second maxilliped (Fig. 6c) : Basal and coxal segments not separated, endopod 5-segmented, 1st segment not completely demarcated from 2nd, 3rd with 1, 4th with 3 dorso-external setae, 5th with 4 setosed spines. Exopod long, stout, 2-segmented, distal segment with 4 plumose setae, epipod short, bilobed.

Third maxilliped (Fig. 7a) : Basis slightly demarcated from coxa, inner margin of coxal segment with 1 spine and 1 seta, ischium with 3–5 acute spines or processes and 6 setae with additional 2 on outer surface ; merus with a small blunt anterio-internal spine on inner surface, merus to dactylus setosed as shown in figure.

Peraeopods, cheliped (Fig. 7c) : Inner margin of ischium/basis with 3 stout curved spines, merus with 3 stout spines, carpus inner margin with 1 small spine, propodus distal half, inner margin sharp, slightly cristate, setal investment as shown in figure. Peraeopods 2–5 (Fig. 8b) dactylus distally spinulate, much longer than propodus + carpus, basis of peraeopods 2–3 with stout curved spine, merus of peraeopods 2–4 and sometimes ischium with long spines decreasing in size distally ; setal and spinule investment as shown in Fig. 8b.

Abdomen (Fig. 8a, 10a) : Sub-cylindrical 5-segmented + telson. Posterio-dorsal margins of segments 2–5 with pair of acute spines (*P.D.*) decreasing in size on successive segments ; segment 3 with 1 pair and 4 and 5 with 2 pairs of additional minute spinules ; dorsal surface of segments 2 and 3 with a median spine. A pair of well-developed pleopods on segments 2–5, exopods (Fig. 9c) long, each with 8 terminal plumose setae ; endopod short with 2 coupling hooks on each pleopod.

FIRST CRAB

Dimensions : *C.L.* 1·4–1·5 mm.

Carapace : Longer than broad, narrowing anteriorly, invested with numerous setae of varying lengths (Fig. 10b). Anteriorly directed frontal horns broader than in megalopa, apices setosed. Hepatic and outer epibranchial regions swollen, each with a spine ; meso-metagastric and cardiac regions swollen, latter with a pair of small tubercules.

Eyes : Large and broad, cornea well developed.

Antennule (Fig. 4g) : Exopod now with 3 incipient segments, terminal with 5 aesthetascs and one seta ; endopod with 3 incipient segments, terminal with 3 setae.

Antenna (Fig. 5e) : Now 7-segmented, flagellum not demarcated from peduncle ; 1st segment longest, inner margin with ventrally directed spine shorter than in megalopa and 2 additional smaller spines on inner margin, outer margin with 2 plumose setae ; 2nd and 3rd segments each with 2 setae, 5th with 1, 6th with 3, 7th with apex indistinctly segmented.

Mandibles, maxillule and maxilla : As in megalopa.

First maxilliped (Fig. 6b) : Coxal segment with 8 setae, no longer bilobed, demarcated from basis which has 11–12 setae, endopod distally expanded into broad lobe with 2–3 marginal setae, epipod longer than in megalopa with 1–2 setae.

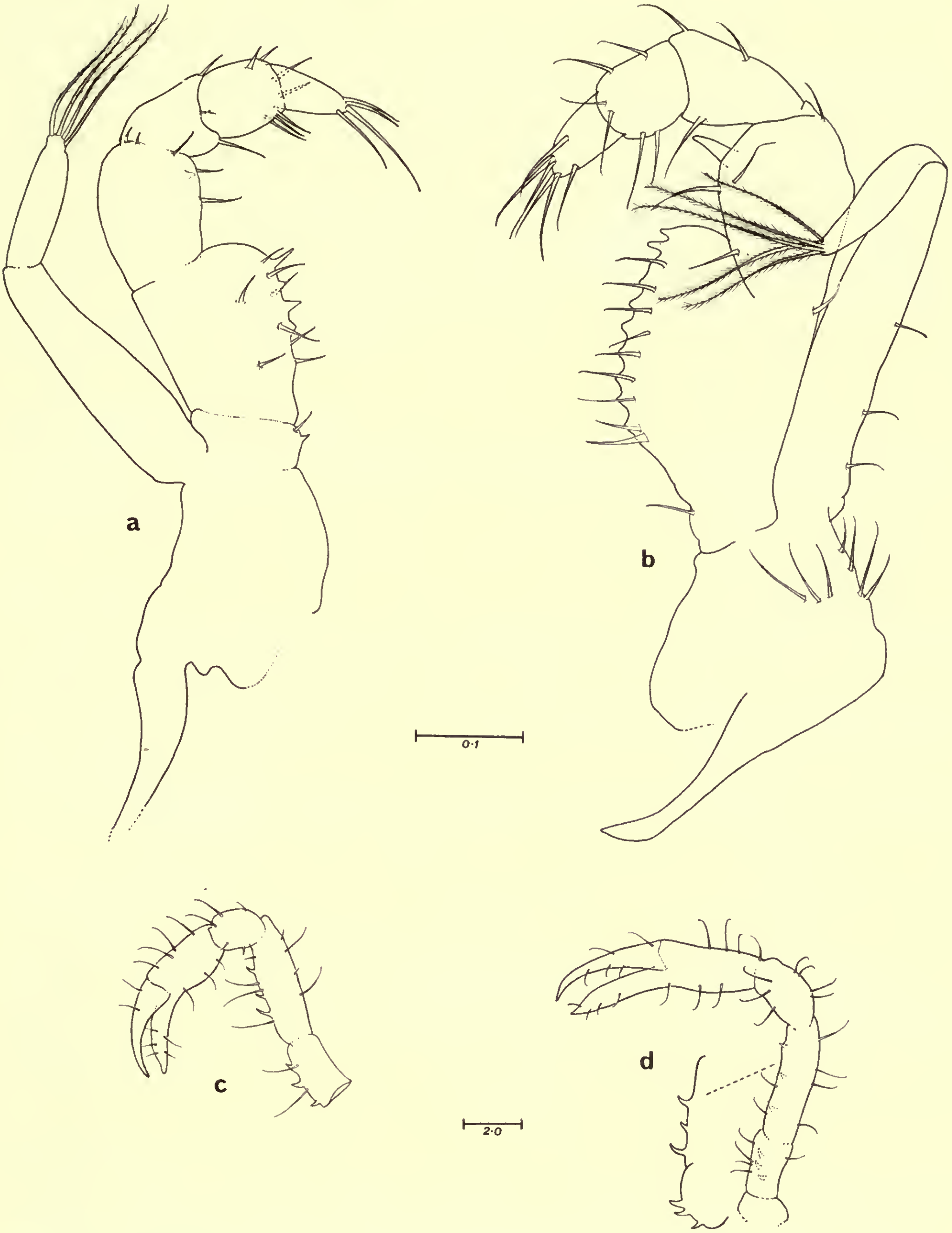

FIG. 7. *Inachus dorsettensis,* third maxilliped of (a) megalopa and (b) first crab; cheliped of (c) megalopa and (d) first crab. Scales in millimetres.

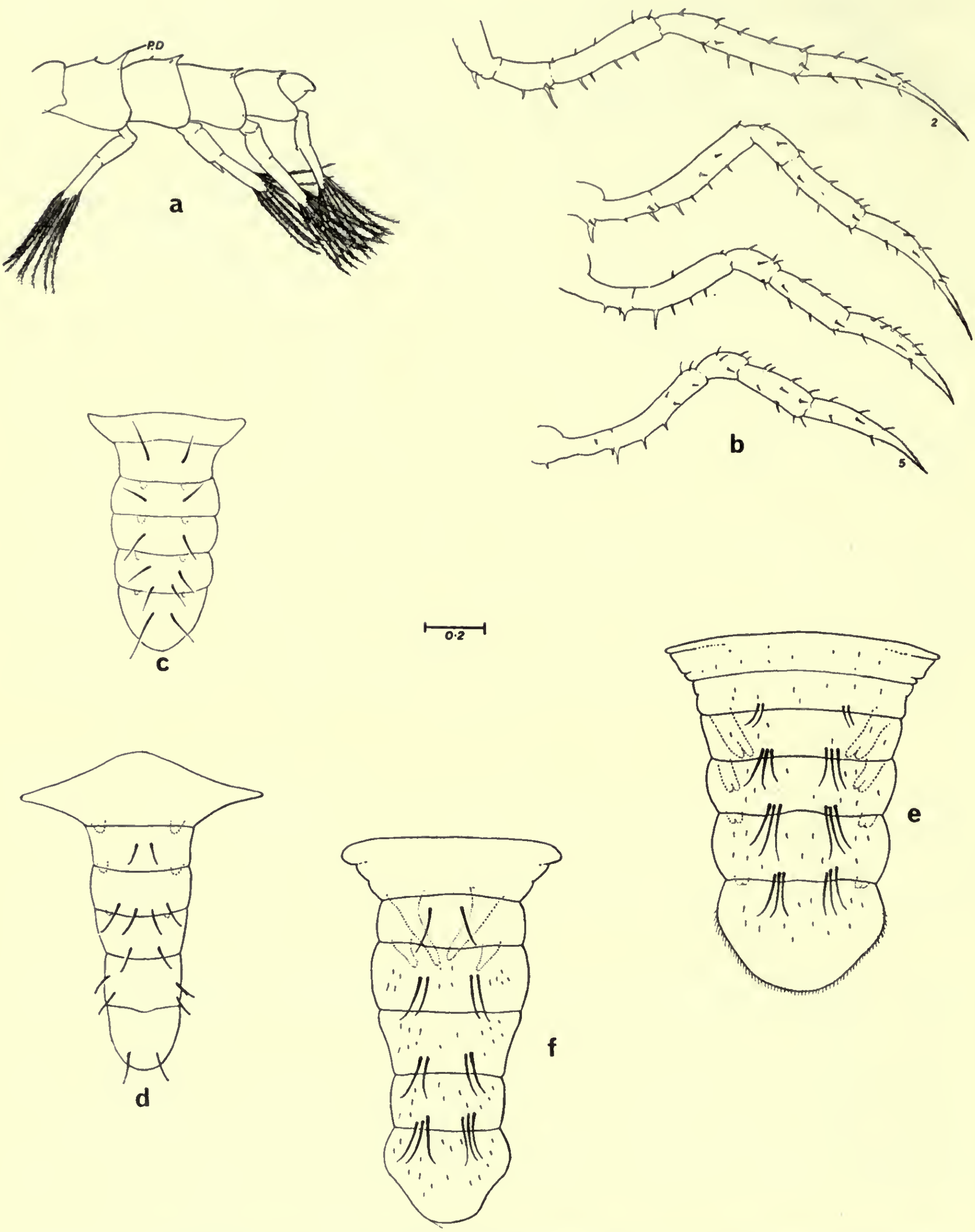

Fig. 8. *Inachus dorsettensis*, (a) abdomen (b) peraeopods 2–5 of megalopa; abdomen (c) of second crab, (d) of third crab ♂, (e) of fourth crab ♀ and (f) of fourth crab ♂. Scale in millimetres.

Second maxilliped : 2nd segment of endopod longer than in megalopa (Fig. 6d), 4th segment now with 4 setae, 5th with 2 setae.
Third maxilliped (Fig. 7b) : Outer margin of basis with 7–10 setae, inner margin of ischium with 9–12 acute or subacute spines and 9–12 setae ; anterio-internal spine on merus now prominent, merus-dactylus setosed as shown in figure.
Peraeopods : Propodus of cheliped (Fig. 7d) less inflated than in previous stage, margins sharp. Peraeopods 2–5 similar, 2nd (Fig. 9d) longest, dactylus of 2nd–4th shorter than propodus, dactylus of 5th (Fig. 9e) same length as propodus and with inner margin bearing 1–2 broad spines, peraeopod setae long.
Abdomen (Fig. 9a, b) : Sub-cylindrical, posterio-dorsal margins of segments 2–5 now with minute spinules and a pair of long setae ; a minute median spine on dorsal surface of telson ; pleopods reduced.

SECOND CRAB

Dimensions : *C.L.* 1·8–2·0 mm.
Description : Unchanged except for abdomen (Fig. 8c) which is now strongly dorso-ventrally flattened and broad. Pleopods on segments 2–5 now reduced to minute buds.

THIRD CRAB

Dimensions : *C.L.* 2·3–2·5 mm.
Carapace : With a pair of well-developed hepatic spines (Fig. 10c) ; setae investing carapace and limbs now strongly hooked at apices.
Abdomen : Male : Narrow (Fig. 8d), well-developed pleopod buds now present near posterior margins of segments 1 and 2, those on segment 3 minute ; no pleopods on segments 4–5.
Female : slightly broader than that of male's ; biramous pleopods present on segments 2–5, but those on segments 4 and 5 very small.

FOURTH CRAB

Dimensions : *C.L.* 2·8–2·9 mm.
Carapace and *limbs* : As in previous stage.
Abdomen : Ventral surface with more setae and margin of 6th segment setosed.
Pleopods : Male – 1st and 2nd pairs (Fig. 8f) much longer than in previous stage.
Female – 2nd and 3rd pairs longer than in previous stage, 4th and 5th pairs still vestigial (Fig. 8e).

FIFTH CRAB

Dimensions : *C.L.* 3·1–3·2 mm.
Carapace (Fig. 10d) : Now with 4 transverse protogastric tubercules and 1 mesogastric ; a pair of mesobranchial and 1 gastric tubercule as in the adult form.
Pleopods : Male – 1st and 2nd now well developed.
Female – Pleopods of the 4th and 5th abdominal segments now much longer and strongly biramous.

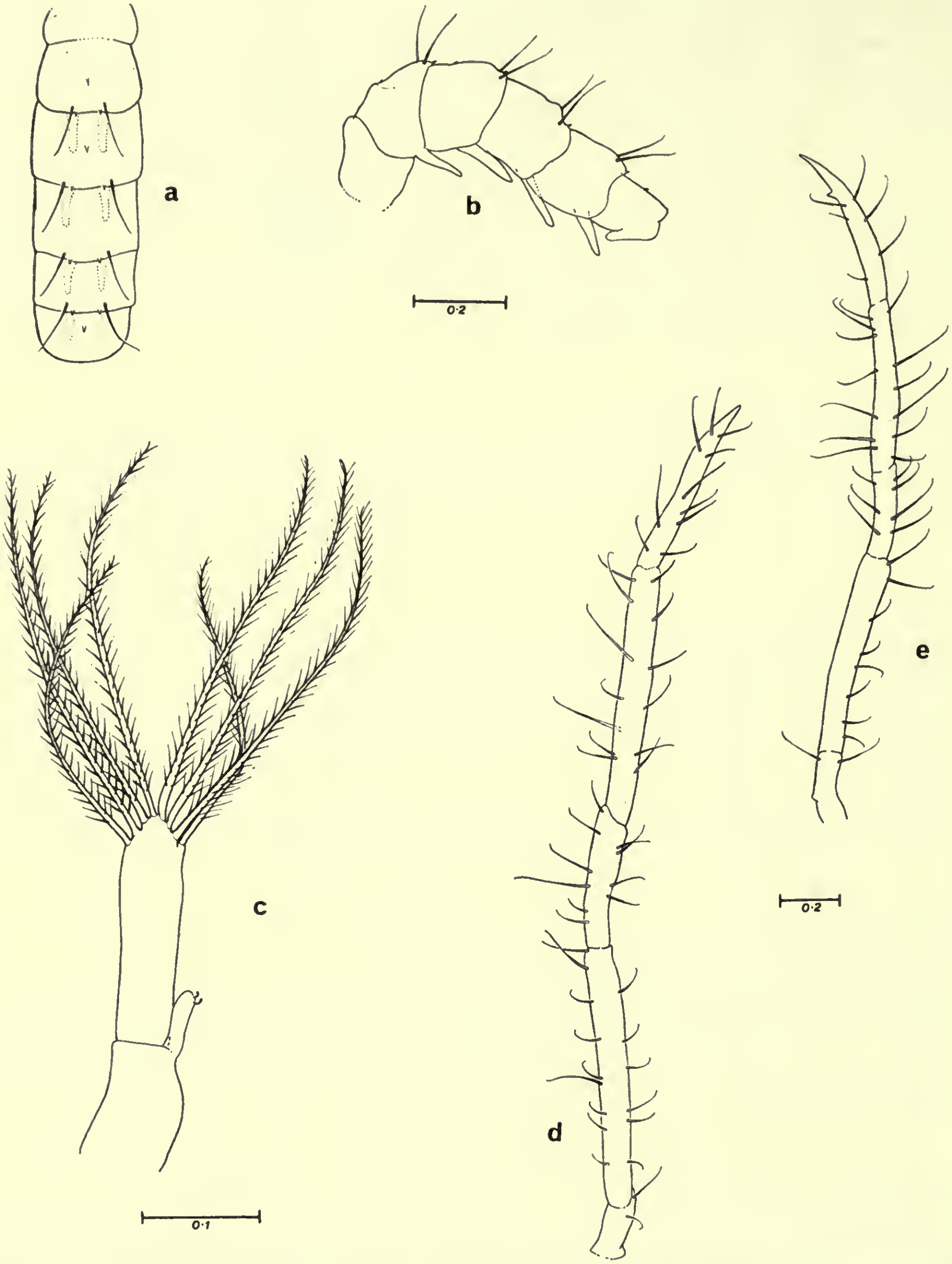

FIG. 9. *Inachus dorsettensis*, abdomen of first crab, (a) dorsal and (b) lateral aspects respectively; (c) 1st pleopod of megalopa; (d) 1st peraeopod of first crab; (e) 5th peraeopod of first crab. Scales in millimetres.

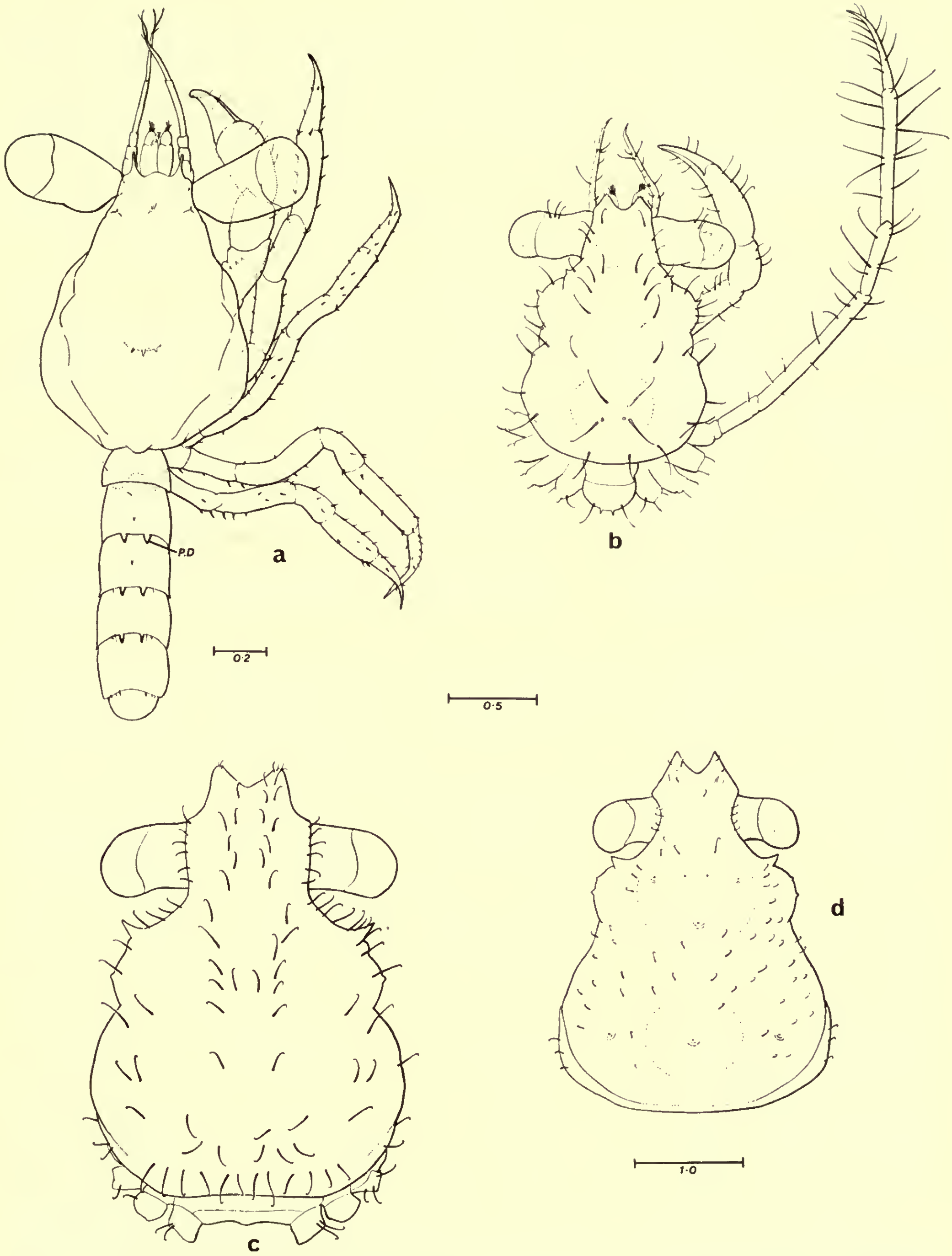

FIG. 10. *Inachus dorsettensis*, (a) megalopa; (b) first crab; (c) third crab; (d) fifth crab. Scales in millimetres.

REMARKS

In Tables 1 and 2 the present material of *I. dorsettensis* is compared with previous accounts of the larval and juvenile stages of this species. Some differences are apparent in setal armature of certain appendages of the first zoeal stages, particularly with reference to the maxillules, maxillae and maxillipeds of Heegaard's Mediterranean material.

TABLE 1

	Claus, 1876	Lebour, 1927; 1928	Heegaard, 1963	Ingle, 1977
		1st zoea		
Dorsal spine:	slightly longer than carapace length, curved	as long as carapace, curved	much longer than carapace, curved	slightly longer than carapace, apically curved
Majid spine:	not shown	not shown	well developed	well developed
Dorso-median elevation of carapace:	slight	pronounced	very pronounced	very pronounced
Antennule:	2 aesthetascs	2 aesthetascs + 1 seta	2 aesthetascs + 2 setae	2 aesthetascs + 2 setae
Antenna, spinous process:	shorter than dorsal spine	shorter than dorsal spine	much shorter than dorsal spine	shorter than dorsal spine
Antenna, endopod/spinous process length:	about ¼	about ¼	between ¼ and ⅓	about ¼
Maxillule, basal endite:	not shown	not shown	with 4 setosed spines and 2 setae	with 5 setosed spines and 2 setae
Maxilla, basal endite:	not shown	not shown	with 8 setae	with 7–8 setae
Maxilla, scaphognathite:	not shown	not shown	with 7 setae, posterior lobe long	with 10 setae, posterior lobe short
First maxilliped, basis:	without setae (?)	without setae (?)	with 3 setae	with 2, 2, 2, 3 setae
First maxilliped, endopod:	0, 1, 2, 1, 3+1	(?) 0, 2, 0, 2, 3+1	2, 2, 1, 2, 3+1	3, 2, 1, 2, 4, +1
Second maxilliped, endopod:	(?)	(?)	2-segmented	3-segmented
Second maxilliped, endopod setae:	(?) 0, 2, 2	(?) 0, 0, 3	0, 0, 2+1	0, 1, 3+1
Abdomen, dorso-lateral processes:	acute	acute	truncate	acute

These differences could be genotypic, resulting from widely separated geographical populations, or phenotypic, since Heegaard's material was reared during spring and summer when Mediterranean water temperatures are much higher than those of British waters. Differences in setal armature are more apparent when Lebour's

TABLE 2

	Lebour 1927; 1928	Ingle, 1977
	2nd zoea	
Antennule :	4 aesthetascs + 1 long seta	3 aesthetascs + 2 long and 1 short seta
Maxillule, basal endite :	plumose seta on outer margin not shown	a well-developed plumose seta on outer margin
Maxilla, basal endite :	with 8 setae	with 9 setae
Maxilla, scaphognathite :	with 20 setae	with 17 setae
	Megalopa	
Carapace :	(?) cardiac region with a tubercule	cardiac region with 3 spines
Antennule, exopod :	with 5 aesthetascs	with 4 aesthetascs and 2 setae
Antennule, endopod :	bud well developed	bud vestigial
Antenna, 1st segment :	spine short, obtuse	spine long, acute
3rd segment :	without a seta	with a seta
5th segment :	with 1 seta	with 4 setae
terminal segment :	with 2 setae	with 3 setae
Abdomen, dorsal spines :	long	short
1st segment :	with lateral setae	without lateral setae
3rd segment ·	without median spinule	with median spinule
	1st crab	
Carapace :	almost as broad as long	much broader than long

account of the second zoeal stage is compared with the corresponding stage of the present material and there are even greater dissimilarities between corresponding megalopal and first crab stages (see Table 2). Such discrepancies are not easily explained, particularly as both Lebour's larvae and the present material were reared during the same months and hatched from females collected in the same area. However, variation in laboratory reared material has received little attention (see Ingle & Rice, 1971 : 284 ; Gonor & Gonor, 1973 : 245).

The first zoeal stage figured by Cano (1893) as *I. scorpio* was referred to *I. dorsettensis* by Lebour (1927) and Heegaard (1963). But this figure clearly shows a globular carapace that is without a dorso-median elevation which are two important features of the first zoea of *I. thoracicus* and Cano's larva, therefore, clearly belongs to this latter species.

At present the larval and early crab stages of *I. dorsettensis* cannot be distinguished from those of *I. phalangium* (= *I. dorynchus*) or from *I. leptochirus*. Although Lebour (1928 : 548) states that the first zoea of *I. leptochirus* has longer lateral telsonic spines than either of the other two species and is more brightly coloured and that *I. phalangium* has a longer dorsal spine than *I. dorsettensis*, she was unable to detect differences between the megalopal stages of these three species except for the 'rostral horns' that are apparently closer together in *I. phalangium* and *I. leptochirus* than in *I. dorsettensis*.

An interesting result of this study of *I. dorsettensis* is that the first pair of pleopod buds of the male appear at the third crab stage and not at the second as described by Shen (1935) for the portunid *Carcinus maenas*. It remains to be seen whether this will be the case when post-larval material of other Majids and Portunids become available for comparison.

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